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PALEOECOLOGY AND ECOMORPHOLOGY OF THE GIANT SHORT-FACED BEAR IN EASTERN BERINGIA

A

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Presented to the Faculty

of the University of Alaska Fairbanks

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DOCTOR OF PHILOSOPHY

By

Paul Edward Matheus, B.A.

Fairbanks, Alaska

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PALEOECOLOGY AND ECOMORPHOLOGY OF THE GIANT SHORT-FACED BEAR IN EASTERN BERINGIA

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ABSTRACT

The short-faced bear (*Arctodus simus*) was a widespread Tremarctine bear indigenous to North America until its extinction around 11,500 BP. *Arctodus* inhabited Pleistocene ice-free refugia in Eastern Beringia (the northwestern limit of its range) until at least 20,000 BP. Because of its gracile, long-legged build and extremely large size, most paleontologists believe this bear was a high-speed pursuit predator which had preyed on the largest herbivores of Pleistocene North America. Alternatively, energetic arguments have been used to suggest that *Arctodus* was too large to be carnivorous and evolved its large size within an herbivorous or omnivorous niche.

To test these competing hypotheses, I reconstructed aspects of *Arctodus*' trophic position and paleodiet by analyzing stable isotope ratios ($\delta\ ^{13}C$ and $\delta\ ^{15}N$) in bone collagen extracted from east Beringian fossils. Other bears and carnivores from Beringia were analyzed to help interpret the results. Isotopes reveal that *Arctodus* was highly carnivorous, it fed on herbivores which consumed C3 vegetation, and it did not eat salmon. The herbivore/omnivore hypothesis is thus rejected.

Predatory hypotheses predict that we should find certain morphological features in a predatory bear which would enhance one or more of the following skills: top running speed, acceleration, or maneuverability at high speeds. I re-analyzed the postcranial morphology of *Arctodus* and used data on running speed and bone strength in other large mammals to show that a bear the size of *Arctodus* with long, gracile limbs would not have been able to endure the extreme dynamic forces incurred during predatory activities. Instead, *Arctodus*' morphology and body size indicate it had evolved to maximize locomotor efficiency using a pacing gait. I suggest that *Arctodus* evolved as a specialized scavenger adapted to cover an extremely large home range in order to seek out, procure, and defend large-mammal carcasses from other carnivores.

By modeling herbivore populations and their mortality, I show that enough carcass biomass was being produced in Pleistocene Beringia to make this scavenging niche energetically feasible. The model helps show that *Arctodus*' extinction probably is best tied to a reduction of year-round carcasses on the landscape, a condition which arose in the Holocene when the herbivore fauna became less diverse and began to experience more seasonal mortality.

EXTENDED ABSTRACT

The giant short-faced bear (*Arctodus simus*) was a widespread Tremarctine (New World) bear indigenous to North America until its extinction around 11,500 BP. *Arctodus* inhabited Pleistocene ice-free refugia in Eastern Beringia (the northwestern limit of its range) until at least 20,000 BP. *Arctodus* was the largest bear and perhaps the largest species of Carnivora that ever lived, yet it was characterized by a gracile post-cranial morphology and it was relatively long-legged. Most ecological models reconstruct this bear as a high-speed cursorial pursuit predator which preyed on a the largest herbivores of Pleistocene North America. However, it also has been argued on energetic grounds that this bear was too large to be carnivorous and evolved its large size within an herbivorous/omnivorous niche. Within both models, the immigration of brown bears into North America during the late Pleistocene has been invoked as a possible cause for the extinction of *Arctodus*.

I extracted fossil bone collagen from east Beringian short-faced bears, brown bears, and other carnivores for stable isotope analysis ($\delta\ ^{13}C$ and $\delta\ ^{15}N$) in order to test competing dietary models and the competition hypothesis. Results reveal that *Arctodus* was highly carnivorous, that its diet was completely terrestrial (i.e., no salmon), and that it fed on herbivores which consumed C_3 vegetation. The herbivore/omnivore foraging model is thus rejected. Stable isotope data from Pleistocene and modern brown bears reveal that Pleistocene brown bears from non-coastal regions of east Beringia were omnivores that relied on terrestrial C_3 vegetation, limited amounts of terrestrial meat, and varying amounts of anadromous salmon running up the Yukon River drainage system (except for bears from the Yukon Territory, which show no signs of salmon eating). Isotopically, this Pleistocene population of inland brown bears most closely resembles modern populations from coastal Alaska that feed on salmon to varying degrees. In contrast, modern inland bears show no isotopic indication of salmon use. Because of the disparate resource base of Pleistocene brown bears and short-faced bears, and the clear physical dominance of *Arctodus*, the competition hypothesis is rejected and it is unlikely that brown bears played any role in *Arctodus*' extinction.

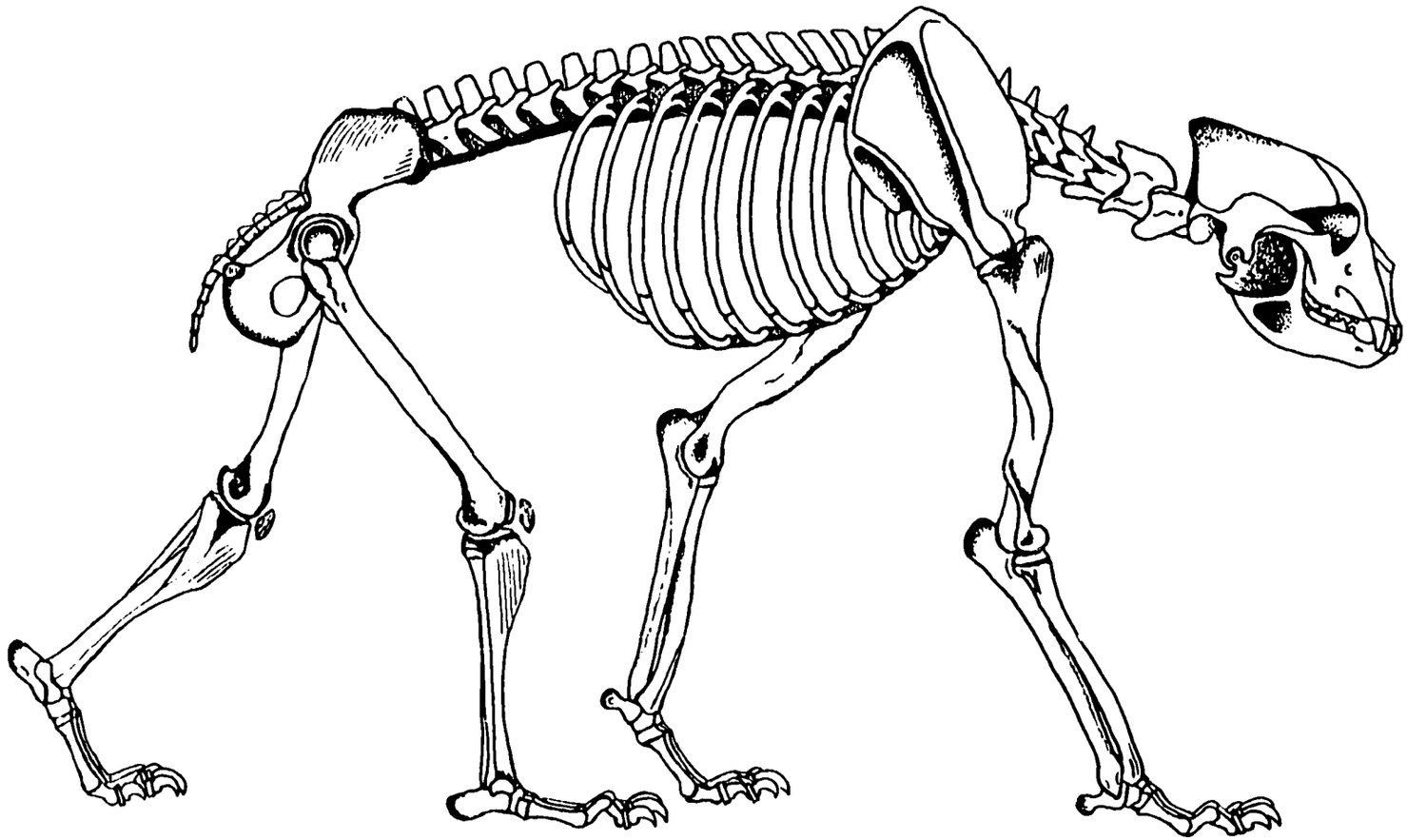
Given the knowledge that *Arctodus* was carnivorous, I re-examined its postcranial morphology and locomotor abilities in order to test predictions of the predatory model. Within this model there are two sub-hypotheses that can be constructed based on the types of prey which were available to *Arctodus*: 1) *Arctodus* preyed on the largest and slowest megafaunal species, or 2) *Arctodus* preyed on faster, moderate-sized megafaunal species. The first hypothesis predicts a large body and strong, robust build in *Arctodus* and must be rejected because of *Arctodus*' gracile postcranial morphology. The second hypothesis predicts that we should find certain morphological features in *Arctodus* which would enhance one or more of the following skills: top running speed, ability to accelerate, or ability to maneuver at high speeds. Data

collected on running speed and bone strength in other large mammals show that a bear the size of *Arctodus* with long gracile limbs would not have been able to endure the extreme dynamic forces incurred at high speeds, during rapid acceleration, or during sharp turns, making it unsuitable as a predator. Therefore, while the first predatory sub-hypothesis accurately predicts *Arctodus*' large size, it does not predict *Arctodus*' gracile build. The second predatory sub-hypothesis is consistent with *Arctodus*' gracile build but cannot explain its large size.

On the other hand, numerous aspects of *Arctodus*' morphology and body size indicate that it was an incipient cursor that had not evolved for speed, but rather for increased locomotor efficiency during prolonged travel. It swung its legs in a more parasagital plane in-line with the body compared to other bears, and it had a short, sloping back with tall front limbs and short hind limbs. This conformation indicates that *Arctodus* evolved to use a pacing gait— a highly efficient, moderate-speed gait. Its large body size and long legs also would have increased locomotor efficiency because these traits increase the amount of elastic strain energy that can be stored and recovered from stretch tendons in mammalian limbs. Considering these facts, I suggest that this carnivorous bear had evolved as a specialized scavenger adapted to cover an extremely large home range in order to seek out broadly-distributed large-mammal carcasses and to dominate this lucrative, but unpredictable carrion resource. Under such a model, there would have been additional selective pressure for increased body size so that *Arctodus* could procure and defend carcasses from other large carnivores, some of which were gregarious.

To test the energetic feasibility of the scavenging hypothesis I developed a model of carcass production on Beringian landscapes based on estimates of herbivore populations and their expected mortality rates. Results indicate that Pleistocene environments would have produced enough carcass biomass from natural mortality and predation by other carnivores to support at least twice the required minimum viable population of short-faced bears. The model helps show that *Arctodus*' extinction probably is best tied to the lack of year-round carcasses on Holocene landscapes, a condition brought on by the Holocene's less diverse herbivore fauna, which is dominated by ruminants experiencing highly seasonal mortality. The Holocene condition produces a seasonal glut of carcasses (late winter-spring) followed by a tight dietary bottleneck (summer-early winter) when few carcasses are available— conditions which led to the demise of *Arctodus*.

It has been suggested that *Arctodus* and other large carnivores in late Pleistocene North America were so large and aggressive that they prevented humans from entering the New World via the Bering Land Bridge until the extinction of these carnivores at the close of the Pleistocene (~ 10,000 - 12,000 BP). Even though I present evidence that *Arctodus* was very large and aggressive, I refute the hypothesis that short-faced bears excluded humans from North America by showing that the terminal date of *Arctodus* in eastern Beringia currently stands at ~ 20,000 BP, which predates the first human occupation of the region by about 8000 years.



*The Giant Short-Faced Bear (*Arctodus simus*) as reconstructed by author*

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PREFACE

The five chapters constituting the body of this thesis were not written sequentially in the form of a conventional thesis. Chapter 1 is a paper published early on in this project to report my initial stable isotope data and paleodietary conclusions regarding short-faced bears and Pleistocene brown bears in eastern Beringia. It was published before my ideas on the morphology of *Arctodus* were solidified. Consequently, Chapter 1 uses the stable isotope data as a springboard to propose a new model for the niche and ecomorphology of *Arctodus*, and it is somewhat speculative.

I test the ecological model of Chapter 1 more thoroughly in Chapters 2, 3, and 4. These three chapters were written as a single unit and represent a heuristic approach to deciphering the morphology and lifestyle of an extinct and extraordinary animal. The reader may find these chapters long and heavy in explanatory prose as I try to weave specific data on *Arctodus* with theoretical discussions on body size and form into a discourse on what it means to be a large, carnivorous mammal. However, I felt this was necessary both to document the thought process behind my specific conclusions and to demonstrate the process of inferential reasoning and hypothesis testing used in paleobiological studies. In this day and age of ultra-concise scientific writing, it seems that little room is left in the realm of published literature to fully explore the ideas behind first principles of biology and explain how we go about the biological thought process. The dissertation remains one of the few avenues left for such explorations. But most of all, I hope this compilation of data and knowledge (both my own and that of others) may be useful to researchers studying similar questions of large mammal locomotion and ecomorphology.

Chapter 5 is another independent manuscript which discusses the ramification of *Arctodus*' ecology and behavior on human migrations into the New World. It was prepared as an invited paper and is being published in a refereed conference proceedings volume. Like Chapter 1, the fifth chapter was written before Chapters 2, 3, and 4, and it too is less specific than they are regarding my assessments of *Arctodus*' morphological adaptations. However, Chapter 5 contains a concise summary of my reconstruction of *Arctodus*' paleoecology.

Subsequent to the publication of Chapter 1, I collected additional stable isotope data on Pleistocene and modern carnivores that substantiate and add to the conclusions of that paper. Appendix 1 lists these data and provides a brief discussion of their implications. Appendix 2 is a manual for extracting collagen from fossil and modern bone detailing the methods I used and developed in this research. It was written as a detailed, step-by-step protocol because I have received multiple requests for instructions on these techniques which are more explicit than those described in the Methods section of published papers. Hopefully, this manual fulfills that need.

I am the sole author of all chapters in this thesis, including the two published manuscripts.

ACKNOWLEDGMENTS

Most acknowledgments *end* by mentioning a spouse or other family member whose support was critical for completing a thesis. However, I want to *begin* my acknowledgments by thanking my special person— Toos— for being the best companion anyone could have. Be it on the trail or just driving home every day after work— Toos, you kept me going.

Professionally and personally, Dale Guthrie has inspired me in ways beyond the role of a graduate advisor, and he has been the principle element in my formation as a scientist. There was not a single time when I walked into Dale's office to talk about this thesis that the subject did not quickly change to something more interesting, and I thank him for that. It was those tangential discussions and the subjects they led to which formed the most valuable part of my education at UAF. I also want to thank Dale for showing me by example that you learn about nature empirically and for re-enforcing the idea that you become a good biologist by spending time in the woods.

The professors who sat on my graduate committee are crack scientists whose opinions I have valued greatly. Thanks to Don Schell, who not only introduced me to the use of stable isotopes in ecological research, but also reminded me— whether I liked it or not— that marine ecosystems dominate this planet (but Don, I still think there are isotopic gradients in terrestrial systems). Richard Scott was one of the few people on campus who I could sit down and talk to about all the old names in evolutionary theory, like Simpson, Mayr, Goldschmidt, Wright, Williams, etc.. And Richard's proseminar in Physical Anthropology— one of the first classes I took at UAF— will always stand out in my mind as an important formative experience. Finally, let it be known that Mary Edwards— UAF's workhorse who sits on practically every Quaternary graduate student's committee— is not the "Mother Hen" she thinks she is. Rather, she is a caring person, the best editor anyone could ask for, and a role model for how co-operative research should be done.

I would like to thank the people of Alaska who have collected fossils and donated them to the University of Alaska Museum. Their generosity allows the rest of us to learn more about Alaska's past. I especially thank the Gelvin family of Birch Creek for allowing me to sample and measure a short-faced bear fossil they collected, and Nancy Klemm, who allowed the same treatment of a brown bear fossil her husband collected on the Colville River.

Various departments and staff members at the University of Alaska Museum have been gracious facilitators of this work. Joe Cook, curator and chairman of the Mammal Department, allowed me to collect bone samples from the department's world-class collection of bear skulls, and he loaned me bones for study. Gordon Jarrell was very kind in letting me access the mammal collection at my convenience (not his), and while this thesis addresses the consequences of large body size, Gordon was a constant

reminder that some of the most interesting mammals weigh less than 1 kg. I thank Roland Gangloff, curator of Earth Sciences, for allowing me to examine and borrow specimens from the paleontology collection on numerous occasions.

Most all of the fossils studied during this research are housed at the American Museum of Natural History, New York. Richard Tedford, curator and former chairman of the Department of Vertebrate Paleontology , was extremely generous in allowing me to access, study, and sample bones at all hours of the day (and night) during my visits to the department's Alaskan collection. Dr. Tedford ran a superb department whose foremost goal is to gain new knowledge about the species represented in its collection. I thank Ross MacPhee, curator and chairman of the Department of Mammalogy, for the serious deliberation and consent he gave to my request to collect bone samples from the valuable African carnivores curated by his department. That was no small request on my part.

Dick Harington, the foremost authority on Canada's Quaternary mammals and curator of Paleobiology at the Canadian Museum of Nature, has extended many gratuities to me. Not only did he allow me to study and sample fossils from the Yukon Territory housed in the CMN's collection, but he was a kind and fun companion on the Kolyma River when I was a green and budding paleontologist. I still pattern many of my field habits after Dick. Dick also has graciously allowed me to use some of his unpublished radiocarbon dates on Arctodus in this thesis. Any citation of those dates should credit C.R. Harington directly.

Back when I did not know a collagen molecule from a bowl of jelly, Tom Stafford at the Institute of Arctic and Alpine Research, University of Colorado, let me spend a marathon week at his lab learning the techniques and nuances of collagen extraction. Tom is one of those brilliant scientist who is as much an engineer as he is a researcher, and the most valuable lesson I learned from him may have been how to just pick up a condenser and a dewar of liquid nitrogen and build your own lyophilizer when the $10,000 commercial one breaks down. Without my experiences in Tom's lab, I would not have been able to set up my own collagen-extracting facilities at UAF.

The Department of Biology and Wildlife at UAF funded me for many semesters through teaching assistantships and instructorships, and I thank them for those opportunities. Through those experiences, I not only supported myself, but I learned about the art and science of teaching— the most important job we do at a university. I also would like to thank the various department heads, directors, and deans at The Department of Biology and Wildlife, The Institute of Arctic Biology, and The former College of Natural Sciences who contributed funds to my research during times when money was very tight. Way back when this project started, the Graduate School awarded me a Natural Resources Fellowship which allowed me to spend time setting up laboratory facilities and developing my protocol. I thank The Graduate School for that support and for granting me a Thesis Completion Fellowship in my final year of writing. The UA

Museum's Geist Fund provided me with critical funding almost on a yearly basis. Their grants allowed me to indulge in many projects either directly or tangentially related to my thesis research. Don Schell generously sponsored my first trip to the AMNH and the CMN in 1991. When I had nowhere to set-up and perform my laboratory analyses, Ron Smith was kind enough to offer me lab space at the cost of his own working space— thanks Ron. When I ran out of funding during the final push of my laboratory work, The Alaska Quaternary Center kept my research going with an emergency grant. The AQC also has been a source of moral support over the years, and a good place to call home.

In 1990, I spent two months as a member of a paleontological expedition in northeastern Siberia sponsored by the Russian Academy of Sciences and organized by Andrei Sher. This adventure will reign as one of the most impressionable and lasting experiences of my life. I want to thank Andrei for organizing the expedition and Dale Guthrie for inviting me to accompany him on that trip. The expedition occurred during the last year of the Soviet Union's existence, and now that Soviet support for the sciences is all but gone, such grand, old-fashion expeditions are no longer undertaken in Russia. I am thankful to have been part of such an adventure, the likes of which may be gone forever.

Anyone who undertakes a dissertation benefits from the advice and generosity of people who have no official connection with the project. I have mentioned only a few in my case, but there were many, including numerous friends and fellow graduate students. The core and spirit of Quaternary research at UAF still emanates from Dave Hopkins, and I feel privileged to have had opportunities to discuss the Quaternary with him and glean information from his vast warehouse of ideas. Craig Gerlach has been an inspiration and role model through his tireless dedication to teaching, research, and leading the Alaska Quaternary Center. Even more, Craig inspires enthusiasm and creative thought in paleo-research through his own open-minded approach to science. I also want to make sure I thank the staff of the Owen K. Mason Library. Its doors were never closed and my card never expired; it was an invaluable resource during this research. Thanks Owen.

Finally, I recall a thesis defense years ago by a graduate student who thanked his mother for nine months of agonizing gestation and a painful parturition, and then (in jest) thanked his father for the grand gesture of donating a Y-chromosome. I lack such a witty way to thank my parents for all they have done, but their support has meant a lot to me.

CHAPTER I

THE DIET AND CO-ECOLOGY OF SHORT-FACED BEARS AND BROWN BEARS IN EASTERN BERINGIA: STABLE ISOTOPE DATA AND A RECONSIDERATION OF *ARCTODUS'* FORAGING BEHAVIOR[1]

ABSTRACT

Carbon and nitrogen stable isotope analyses of fossil bone collagen reveal that Pleistocene short-faced bears (Arctodus simus) *were highly carnivorous in Beringia, while contemporaneous brown bears* (Ursus arctos) *had highly variable diets that included varying amounts of terrestrial vegetation, salmon, and moderate amounts of terrestrial meat. A reconsideration of* Arctodus' *highly derived post-cranial morphology suggests that these huge bears had evolved towards increased locomotor efficiency and sustained travel, not for fast running, acceleration, or maneuverability. The latter traits are necessary requisites, to varying degrees, for a predator. Therefore, the most parsimonious reconciliation of isotopic and morphological data is that short-faced bears were not predatory, but instead foraged as wide-ranging scavengers which specialized in finding, procuring, and defending large mammal carcasses from other Pleistocene carnivores.* Arctodus' *efficient locomotion allowed it to search for carcasses economically over a very large home range, and its large size would have made it the dominant carnivore in North America.* Arctodus' *cranial morphology indicates an ability to thoroughly process large mammal carcasses, especially cracking thick cortical bone. This reconstruction of* Arctodus' *foraging ecology and the isotope data for both bear species do not support the hypothesis that competition from brown bears was a significant factor in* Arctodus' *extinction.*

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[1] published as: Matheus, P. E. 1995. Diet and co-ecology of short-faced bears and brown bears in eastern Beringia: stable isotope data and a reconsideration of *Arctodus'* foraging behavior. *Quaternary Research* 44:447–453. (minor revisions added)

INTRODUCTION

Our inability to determine basic aspects of the short-faced bear's (*Arctodus simus*) diet has precluded paleontologists from agreeing on the role of this important, yet enigmatic, species in Pleistocene communities of North America. Debate has focused primarily on *Arctodus'* degree of carnivory versus herbivory and the subsequent adaptive nature of its highly derived morphology, particularly its large size. Kurtén (1967a) proposed that *Arctodus* was a fast cursorial predator, based on its limb morphology and powerfully configured jaw. Most authors agree in general with Kurtén that *Arctodus* was carnivorous and probably an active predator (e.g., Harington 1973, 1977, 1996; Agenbroad and Mead 1986; Voorhies and Corner 1982, 1986; Guthrie 1988; Stock and Harris 1992; Gillette and Madsen 1992; Churcher *et al.* 1993; Richards *et al.* 1996). In contrast, Emslie and Czaplewski (1985) contended that *Arctodus* was omnivorous, but primarily herbivorous, based on morphological similarities with its closest extant relative, the spectacled bear. These authors also used scaling arguments to question whether such a large mammal could function as a carnivore. Furthermore, they disputed Kurtén's assertion that *Arctodus* was cursorily adapted. There are inadequacies and inconsistencies with both the predator and herbivore models, as neither can explain all aspects of *Arctodus'* morphology, and they do not completely reconcile its ecology within the Pleistocene large mammal community.

Despite our lack of knowledge concerning the basic resource requirements of short-faced bears, it also has been hypothesized that competition from brown bears (*Ursus arctos*) may have been responsible for *Arctodus'* demise (Kurtén and Anderson 1974, 1980; Harington 1977, 1980; Richards *et al.* 1996). Brown bears probably immigrated into eastern Beringia from Asia during marine isotope stage 3 or 4, at the latest, but they did not reach areas of North America south of the continental ice masses until about 12,000 yr ago (Kurtén 1960, 1963, 1966a, 1968, 1973a, 1976a; Guilday 1968; Kurtén and Anderson 1974, 1980; Harris 1985). This means the two bears co-existed for many millennia during the Wisconsinan glacial age in eastern Beringia, suggesting that factors other than competition contributed to *Arctodus'* extinction.

In this paper I present stable carbon and nitrogen isotope data obtained from fossil bone collagen of late Pleistocene short-faced bears and brown bears, and compare them to values derived from modern brown bears and other fossil Carnivora. Stable isotopes are powerful tools for interpreting paleodiets (Fig. 1), but they have limitations. In terrestrial systems, $\delta^{15}N$ is useful primarily as an indicator of a consumer's trophic position, because the preferential excretion of ^{14}N (in urea) during protein catabolism increases the relative amount of ^{15}N in a consumer's tissues approximately 3 ‰ over its diet (i.e., 3 ‰ for each trophic step) (DeNiro and Epstein 1981, Schoeninger and DeNiro 1984). Carbon isotopes usually are not significantly fractionated by trophic processes, although there can be a tendency for ^{13}C to become

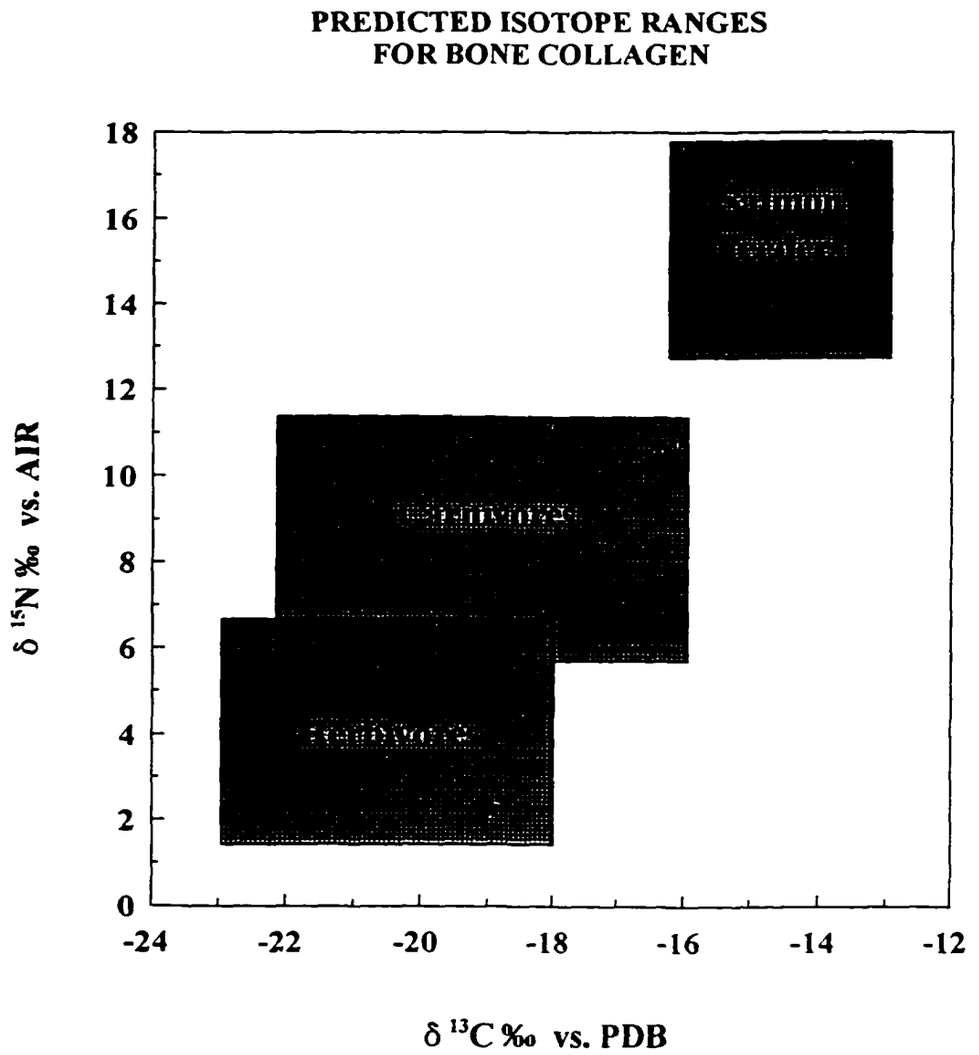

Figure 1. Predicted isotopic signatures for bone collagen in consumers, reflecting dietary and trophic considerations relevant to bears. Ranges were compiled from published data sets with particular consideration of isotope values in modern Alaskan ecosystems.

slightly depleted as it flows up trophic levels (DeNiro and Epstein 1978, Chisholm *et al.* 1982, Chisholm 1989, Schoeninger and DeNiro 1984). $\delta^{13}C$ is more useful as an indicator of carbon fixation pathways in an ecosystem's primary producers, and in the case of secondary consumers, $\delta^{13}C$ can sometimes suggest the types of prey being consumed. For example, in certain ecosystems predators consuming prey that were browsers can be differentiated from predators that consumed grazers (e.g., Tieszen *et al.* 1979a, Tieszen and Imbamba 1980, Ambrose and DeNiro 1986). In addition, both $\delta^{15}N$ and $\delta^{13}C$ can be used to distinguish marine diets from terrestrial diets, or diets which are intermediate (Fig. 1) (Chisholm *et al.* 1982, Schoeninger and DeNiro 1984). This means stable isotopes can be used to determine the relative contribution of salmon— essentially a marine organism— to the diet of bears.

The data presented in this paper elucidate some important aspects of Pleistocene bear diets in terms of trophic position and salmon use. Furthermore, in the discussion I present a model of short-faced bear foraging behavior that is the most parsimonious integration of the isotope data and *Arctodus*' morphology (first proposed in Matheus 1994a, and elaborated on in subsequent chapters). The foraging model predicts that short-faced bears were wide-ranging scavenging specialists that behaviorally dominated other Pleistocene carnivores. Within this model, I conclude that competition between brown bears and short-faced bears probably was insignificant, and played no role in the extinction of *Arctodus*.

METHODS

Collagen was extracted for isotopic analysis from the well-preserved fossil bones of 16 short-faced bears and 14 brown bears from central Alaska (U.S.A.) and west-central Yukon Territory (Canada). To help interpret this data, isotope values were obtained for various populations of modern Alaskan brown bears and from fossils of other Pleistocene carnivores (*Panthera leo atrox*, *Homotherium serum*, *Canis lupus*, and *Gulo gulo*)(data on the latter carnivores presented in Appendix 1).

Radiocarbon dates are available for two of the short-faced bears (NMC 7468 = 26,040 ± 270 yr B.P., TO-2696; NMC 37577 = 29,600 ± 1200 yr B.P., I-11037) (Harington 1977; Harington, C. R., personal communication, 1995). The rest are from sediments generally assigned to the Rancholabrean by collectors, but most probably are Wisconsinan age. Since these sediments are comprised of alluvium of somewhat uncertain age, possibly some of the samples, particularly of *Arctodus*, are older.

Individual bone samples varied from 0.60 to 2.10 grams. Amino acid analysis using high performance liquid chromatography indicated that the acid-insoluble portions of the fossil bones were collagenous (unpublished data). Fossil samples were scraped clean of external residue, soaked in acetone and/or ethanol to remove preservatives, and sonicated. Most samples were crushed into 0.5 to 2.0 cm pieces, but some were powdered prior to demineralization. Modern bones were degreased through

multiple extractions with 100% chloroform.

Procedures for extracting and processing the collagen were adapted from Stafford *et al.* (1988, 1991). The cleaned, crushed bones were demineralized in weak HCl (1 N) at 5° C for 1 to 4 days, depending upon particle size and resistance to demineralization. The non-soluble extracts of fossil bones were soaked for 24 hours in 0.05 M NaOH at 17° C, which removes some organic contaminants, and rinsed to neutral pH. All bones were then gelatinized in weak HCl (pH 3) under N_2 gas at 105° C until it appeared all potential collagen was in solution (4 to 10 hours). The solution was centrifuged and filtered with a 0.45 micron PTFE filter and the supernatent (dissolved collagen) was lyophilized and weighed to determine the percent of collagen recovered. This concluded treatment for modern bones.

Fossil samples were subjected to additional chromatographic separation to remove persistent soil contaminants. In this procedure, the fossil collagen extracts were hydrolyzed in 6N HCl for 4 hours at 120° C (under N_2 gas). The hydrolyzate was passed by gravitational flow through a 2 cc. column of compacted Serva XAD-2 HPLC resin (which retains persistent humates and other categories of organic contaminants), and filtered through a 0.45 micron PTFE filter. The eluate was dried by rotary evaporation.

^{13}C and ^{15}N content were measured on the collagen of modern samples and on the resin-extracted hydrolyzate of fossil samples using a Europa 20-20 continuous flow mass spectrometer. Carbon isotope values are reported as $\delta\ ^{13}C$ versus the PDB standard and nitrogen isotope values are reported as $\delta\ ^{15}N$ versus atmospheric ^{15}N (AIR). A bivariate plot of $\delta\ ^{13}C$ vs. $\delta\ ^{15}N$ was constructed and a Multiple Response Permutation Procedure (MRPP) was used to determine whether apparent dietary distinctions of brown bears and short-faced bears were statistically valid (Zimmerman *et al.* 1985).

Results and Discussion

Bear Diets

Carbon and nitrogen isotope signatures reveal distinct dietary differences between late Pleistocene brown bears and short-faced bears in eastern Beringia (Table 1, Fig. 2). A Multiple Response Permutation (MRPP) test substantiates this conclusion by showing that both bears cluster in two statistically distinct groups based on species assignment (MRPP = -5.84; $p \leq 0.001$).

Most important, $\delta\ ^{15}N$ levels indicate that Beringian short-faced bears were highly carnivorous, functioned primarily as secondary terrestrial consumers, and resided trophically above the large majority of brown bears. Furthermore, *Arctodus* displays a pattern whereby individuals with lower $\delta\ ^{13}C$ values have higher $\delta\ ^{15}N$ values (trend from lower right to upper left in Fig. 2), an indication that short-faced bears were not consuming salmon.

TABLE 1. Isotope values of bone collagen extracted from fossils of late Pleistocene brown bears and short-faced bears in eastern Beringia.

species	collection no.[1]	locality	$\delta^{13}C$	$\delta^{15}N$
brown bear	NMC 29005	Sulphur creek, Dawson, Yukon	-19.57	6.29
brown bear	NMC 38279	Sixty Mile River, Dawson loc. 3, Yukon	-20.00	6.70
brown bear	NMC 47086	Caribou Creek, Dawson loc. 41, Yukon	-19.84	4.36
brown bear	NMC 35965	Hunker Creek, Dawson loc. 16, Yukon	-19.82	4.39
brown bear	FAM 95595	Goldstream Creek, Fairbanks, Alaska	-18.90	6.69
brown bear	FAM 95597	Goldhill, Fairbanks, Alaska	-19.59	6.98
brown bear	FAM 95598	Cripple Creek, Fairbanks, Alaska	-19.11	6.27
brown bear	FAM 95601	Cripple Creek, Fairbanks, Alaska	-20.03	3.30
brown bear	FAM 95610	Fairbanks Creek, Fairbanks, Alaska	-17.36	7.57
brown bear	FAM 95612	Ester Creek, Fairbanks, Alaska	-16.84	12.93
brown bear	AMNH 30421	Fairbanks, Alaska	-19.48	9.94
brown bear	AMNH 30422	Alaska (probably Fairbanks area)	-19.20	10.31
brown bear	AMNH 30780	Goldstream, Fairbanks, Alaska	-19.40	4.44
brown bear	"Colville"	Colville River, Umiat, Alaska	-19.12	9.07
short-faced bear	NMC 7438	Gold Run Creek, Dawson, Yukon	-18.49	10.31
short-faced bear	NMC 36236	Dawson area	-18.07	9.79
short-faced bear	NMC 37577	Hunker Creek, Dawson, Yukon	-18.96	9.74
short-faced bear	FAM 30492	Cleary (Fairbanks), Alaska	-17.80	8.04
short-faced bear	FAM 30494	Ester (Fairbanks), Alaska	-18.14	6.97
short-faced bear	FAM 95607	Ester Creek, Fairbanks, Alaska	-18.10	8.23
short-faced bear	FAM 99209	Ester (Fairbanks), Alaska	-18.12	8.54
short-faced bear	FAM 127688	Goldstream, Fairbanks, Alaska	-17.63	6.60
short-faced bear	FAM 127691	Engineer Creek, Fairbanks, Alaska	-19.04	9.37
short-faced bear	FAM 127699	Goldstream, Fairbanks, Alaska	-18.79	8.57
short-faced bear	AMNH 30494	Cleary Creek, Fairbanks, Alaska	-17.82	7.66
short-faced bear	A-37-10	Upper Cleary (Fairbanks), Alaska	-18.26	9.51
short-faced bear	A-197-2972	Cripple Creek, Fairbanks, Alaska	-18.13	8.37
short-faced bear	A-556	Cleary (Fairbanks), Alaska	-18.49	8.01
short-faced bear	L-gs-33	Goldstream, Fairbanks, Alaska	-18.39	8.25
short-faced bear	"Birch"	Birch Creek, 150 km NE of Fairbanks	-18.07	8.04

[1] AMNH = American Museum of Natural History; FAM = Frick collection, American Museum of Natural History; NMC = Canadian Museum of Nature, formerly National Museum of Canada; "Colville" and "Birch" are from private collections; A- numbers and L-gs are field numbers of specimens in the American Museum of Natural History that do not have collection numbers assigned.

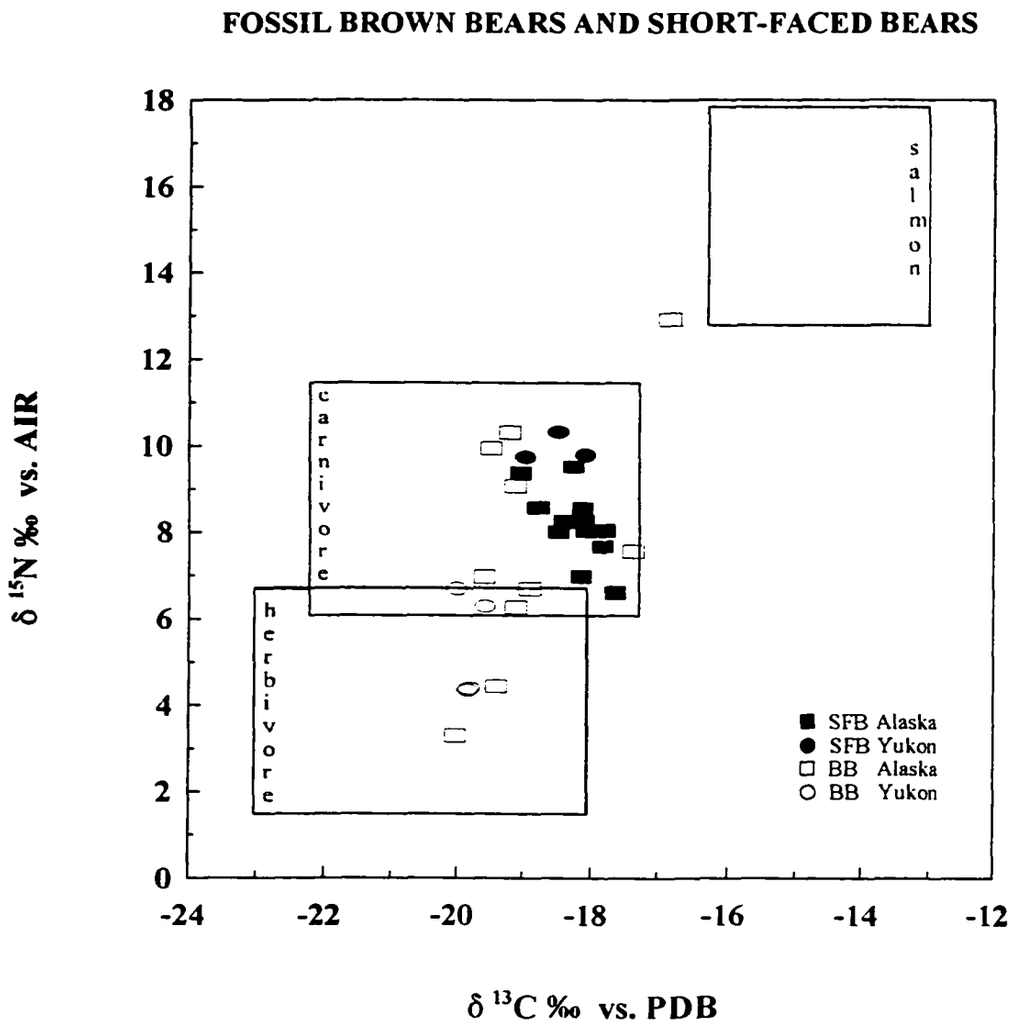

Figure 2. Carbon and nitrogen stable isotope values of bone collagen extracted from fossils of late Pleistocene age brown bears and short-faced bears in eastern Beringia. MRPP statistic (-5.84; $p \leq 0.001$) indicates that each species clusters in an isotopically distinct group, showing that their diets were significantly different. Evidently, short-faced bears were highly carnivorous, while brown bears ate varying amounts of vegetation and salmon, supplemented with occasional terrestrial meat. The data for brown bears displays a trend similar to modern coastal brown bears in Alaska (Fig. 3). Other trends are discussed in the text (*SFB* = short-faced bear, *BB* = brown bear).

TABLE 2. Isotope values of bone collagen (skulls) from two coastal and two inland populations of modern brown bears in Alaska.

collection no.[1]	locality	sex	age (years)[2]	$\delta^{13}C$	$\delta^{15}N$
Admiralty Island					
UAM 13789	Glass Peninsula, Doty Cove	F	10.4	-18.93	9.97
UAM 13791	Pybus Bay	M	7?	-17.04	12.16
UAM 13793	Pybus Bay	M	2.4	-16.91	13.50
UAM 13794	Chiak Bay	F	5.4	-20.04	4.37
UAM 13795	Gambier Bay	M	4.4	-17.77	8.87
ADFG 60	"Alpine Zone"	F	30.0	-21.06	1.13
Alaska Peninsula					
UAM 13943	Meshik River	F	2.4	-19.11	12.39
UAM 13947	Sandy River	M	5.4	-15.67	16.03
UAM 13948	Ilnik River	F	3.8	-18.48	8.91
UAM 13949	Meshik River	M	11.4	-15.59	12.95
UAM 13950	Port Heiden	M	13.8	-15.35	14.10
UAM 13953	Meshik River	F	15.8	-13.90	12.99
UAM 13961	Chignik Lake	?	1.8	-17.14	12.89
Interior					
UAM 2424	Fairbanks area	?	adult	-20.34	5.16
UAM 3394	Twelve Mile Summit	F	5 - 7	-19.17	3.94
UAM 14267	3.5 mile Steese Highway	F	6.5 - 7.5	-20.30	3.51
UAM 14268	Wood River, Alaska Range	M	4.8	-20.00	3.68
UAM 14269	Wood River, Alaska Range	F	14.9	-19.95	4.35
UAM 14270	Nenana	M	7.4	-20.51	4.70
UAM 14271	Bearpaw Creek	M	10.8 - 11.8	-18.47	8.70
UAM 14272	Tanana River, near Manley	F	6.6 - 6.8	-20.14	4.23
UAM 14274	Eagle Summit	M	13.8	-20.55	6.49
UAM 24077	Buzzard Creek, Totatlanika	M	1.5	-20.33	4.86
Brooks Range					
UAM 4825	Upper John River	F	> 5 ?	-19.25	2.86
UAM 9703	Siksikpik Creek	M	"old"	-18.75	5.03
UAM 9704	Masu Creek	M	"old"	-19.29	3.46
UAM 9707	Ukikminilagat	M	"old"	-19.16	4.48
UAM 9720	Inukpasukruk	F	5 ?	-19.81	6.37
UAM 9721	Ukukminilagat	F	4 - 5 ?	-19.65	4.90
UAM 9722	Kallutagiak Creek	M	5 - 6 ?	-18.75	5.45
UAM 9724	Anvik Creek	F	4 - 5 ?	-19.24	3.85
UAM 9725	Ukukminilagat	M	5 - 6 ?	-19.38	5.33
UAM 9726	Anvik Creek	M	5 ?	-19.97	5.86

[1] UAM = University of Alaska Museum, ADFG = Alaska Department of Fish and Game

[2] ages based on number of premolar annuli (measured by ADFG) or estimated (?) by suture closer and tooth wear

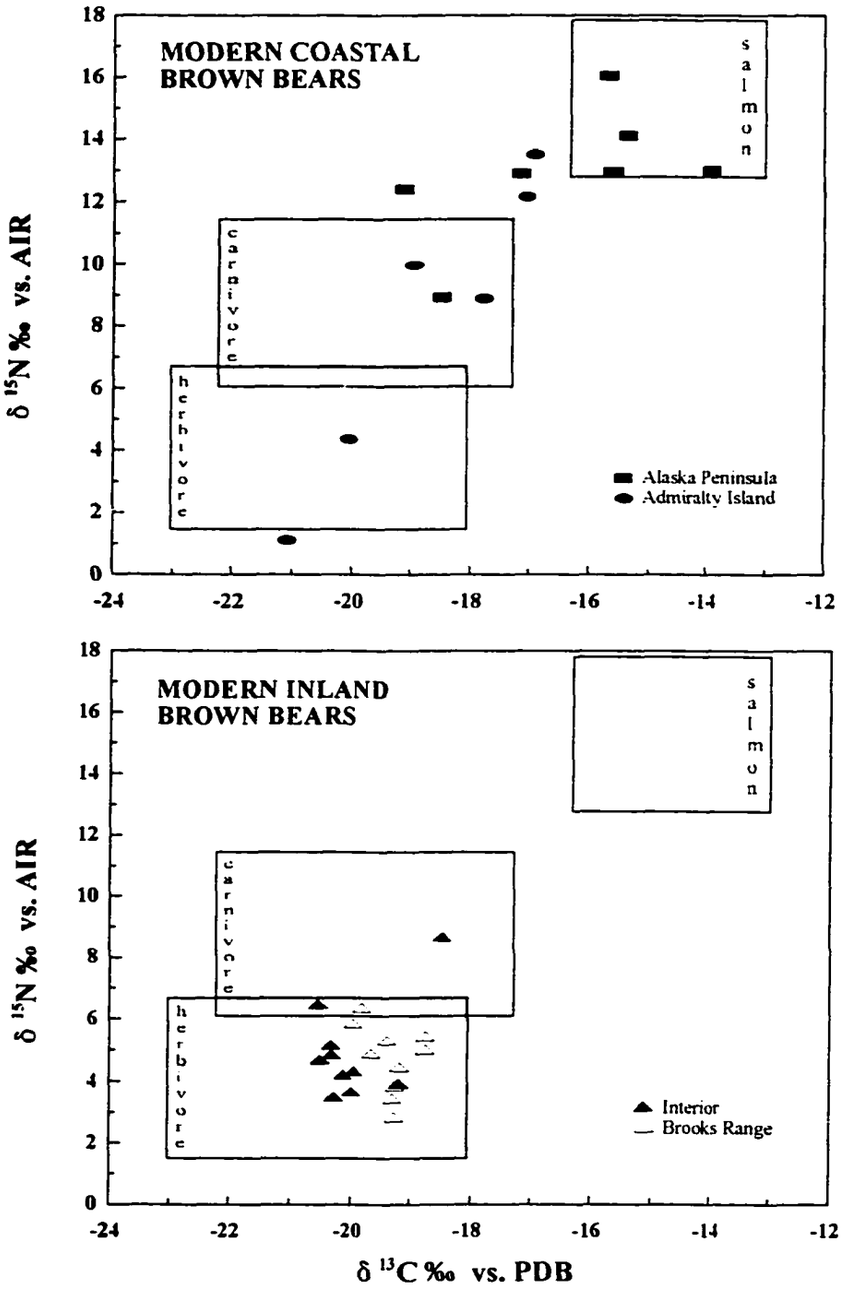

Figure 3. Carbon and nitrogen stable isotope values of bone collagen for two coastal and two inland populations of modern Alaskan brown bears. Isotope values confirm observed dietary differences: Coastal bears are known to feed on varying amounts of vegetation and salmon, and occasionally on terrestrial meat (Schoen *et al.* 1986, Barnes 1989). Inland populations do not feed on salmon and are mostly herbivorous, although individual bears eat differing amounts of terrestrial meat (Pearson 1975, Phillips 1987). Fossil brown bears from interior Alaska (Fig. 2) have isotopic signatures resembling modern coastal bears, indicating that salmon formerly were an important dietary item for interior bears.

The degree of isotopic scatter in short-faced bears suggests that they consumed a diversity of herbivore flesh. Reasoning for this conclusion lies the fact that the isotopic composition of herbivores reflects isotopic levels in the plants they consume, and this gets passed on to predators (Rundel *et al.* 1988). In ecosystems where woody plants are C_3 photosynthesizers and grasses are C_4 photosynthesizers, browsers and grazers can be separated based on $\delta\ ^{13}C$ levels (Tieszen *et al.* 1979a, Tieszen and Imbamba 1980, Ambrose and DeNiro 1986). During full glacials, no trees and few woody plants inhabited Beringia (Guthrie 1990a), so it is unlikely that the variation in short-faced bear isotopes reflects the degree of grazers and browsers in their diet. Within modern arctic vegetation however, there is considerable variation in both $\delta\ ^{13}C$ and $\delta\ ^{15}N$ of plant tissues (Schell and Ziemann 1989, Barnett 1994), and isotope levels vary within taxa due to habitat characteristics such as slope, drainage, and aspect (Barnett 1994). For instance, arctic herbs are lighter in ^{13}C than arctic shrubs. Therefore, while it is impossible to say which specific types of prey *Arctodus* was eating without an exhaustive survey of isotopes in Pleistocene herbivores, it is reasonable to conclude that they were eating a diversity of herbivore flesh.

The isotope data on Beringian brown bears indicate that individual diets were variable, but with a distinct clinal trend (Fig. 2). One primary component of brown bear diet was terrestrial vegetation, but commensurate rises in both $\delta\ ^{13}C$ and $\delta\ ^{15}N$ (trend from lower left to upper right in Fig. 2) strongly suggest that salmon were an important dietary item for some individuals. Some of the rise in $\delta\ ^{15}N$ almost certainly reflects terrestrial meat in brown bear diets, but the influence of salmon seems stronger because of the commensurate rise in $\delta\ ^{13}C$, which is the same pattern displayed by modern populations of coastal brown bears (Table 2, Fig. 3). Coastal bears are known to eat varying amounts of salmon and vegetation, with individual habits varying among bears, often on the basis of age and sex (Schoen *et al.* 1986, Barnes 1990). Variation in the amount of salmon in the diet of coastal bears is readily apparent in their isotopic signatures (Fig. 2). In contrast to modern coastal brown bears, modern inland brown bears have isotopic signatures typical for a terrestrial-feeding species where individuals varied in the amount of meat they ate, but none ate salmon (Fig. 3). Many of these modern inland samples come from essentially the same locations as the fossil samples (Tables 1 and 2), so it seems reasonable to conclude that salmon formerly were a more important resource for inland bears in the not-so-distant past.

Both brown bears and short-faced bears display prominent geographic trends in their isotope ratios. First, fossil brown bears from the Yukon Territory are noticeably lighter in both ^{13}C and ^{15}N — that is, they have a more terrestrial signature— than those in Alaska. The most likely interpretation of this pattern is that Alaskan brown bears had access to salmon, whereas the Yukon bears did not. Today, there does not seem to be much difference in salmon availability between these two regions, as there are modest salmon runs to both areas. The most likely explanation for the Pleistocene pattern is that recurrent ice damming of the Porcupine River and resultant back flooding of the Old Crow Basin (Thorson and Dixon

1983, Thorson 1989, Duk-Rodkin *et al.* 1996) prevented salmon from running into the upper Yukon River system during Pleistocene full glacials. If this is true, these data are indirect evidence that Pleistocene salmon ran up the Yukon River drainage only about as far as the Alaska-Yukon border.

Isotope values for short-faced bear also differ between Alaska and the Yukon Territory, but a direct mechanism for this difference is not apparent. The three short-faced bears from the Yukon had the highest $\delta^{15}N$ levels and some of the lowest $\delta^{13}C$ values of all short-faced bears tested. Theoretically, this pattern could be an indication that short-faced bears in the Yukon resided at even higher trophic levels than bears in Alaska, but this is not a satisfactory explanation. First, the only way for short-faced bears to reside above the level of secondary consumers would have been to regularly feed on other carnivores (or invertebrates). Such an argument would be difficult to corroborate, as there is no comparable situation today. Plus, terrestrial systems rarely support so much trophic depth in food webs where vertebrates eat vertebrates (Pimm 1982, Briand and Cohen 1987). (NMC 7438, which has the highest $\delta^{15}N$ value, was a huge bear and is the type specimen of *A. simus yukonensis*.)

While these geographic differences in isotope values might reflect a certain amount of trophic or dietary variation in short-faced bears, it may be more likely that they indicate subtle differences in the isotopic composition of the primary producers at the base of the food chain between the two regions. As discussed above, isotope levels in plants often vary spatially within ecosystems, responding to differences in eco-physiological mechanisms, topography, and geomorphology (Rundel *et al.* 1988, Lajtha and Marshall 1994). With additional isotope data on a greater variety of consumers, it may be possible to reconstruct specific differences in the past vegetation and environment of Alaska and the Yukon Territory.

Testing The Competition Hypothesis

The hypothesis that brown bears outcompeted short-faced bears assumes that they shared a common, limited resource. In all likelihood, this would have been dietary meat. For most brown bear populations today, productivity seems to be correlated with the abundance of high quality food in their diet, particularly seasonally available meat or salmon, and their preference for meat is well-known (Rausch 1963, Pearson 1975, Schoen *et al.* 1986, Barnes 1990). In Fig. 2, it appears at first glance that there is considerable isotopic (and thus dietary) overlap between brown bears and short-faced bears in the region of the graph characteristic of terrestrial carnivory— i.e., in bears with high $\delta^{15}N$ (compare Fig. 2 to Fig. 1). But, as I described above, the directional trends and clustering patterns are different for each species, and the isotopic values therefore converge in this region for different ecological reasons: brown bears with high $\delta^{15}N$ were eating mostly salmon and vegetation and probably some terrestrial meat, whereas short-faced bears with high $\delta^{15}N$ were simply pure terrestrial carnivores.

Based on these strong dietary distinctions between short-faced bears and brown bears, it is

unlikely that they engaged in significant direct (interference) competition for food resources. But, considering the short-faced bear's carnivorous diet, and the brown bear's known preference for meat, it is probable that both bears shared a preference for meat resources and engaged in limited indirect (exploitative) competition. Considering the size difference between these two bears (see below) and the fact that isotope data indicate that short-faced bears were not denied access to meat resources, it is likely *Arctodus* was the dominant species and was not competitively displaced. Any potential competition would have been resolved via brown bears, the subordinate species, taking on an opportunistic diet consisting of high-quality, seasonally available vegetation supplemented by salmon and occasional terrestrial meat sources. This characterization could describe brown bears in Beringia today equally well, except that inland bears do not eat much salmon.

Arctodus as a Scavenging Specialist

Stable isotopes reveal that *Arctodus* was strictly carnivorous in eastern Beringia, but the isotope data do not reveal how short-faced bears foraged, what specific food items they ate, or how they fit into Pleistocene mammal communities and the region's large carnivore guild. Considering the isotope data, potential competition from other large carnivores, the niches available in Pleistocene ecosystems, and *Arctodus'* highly derived morphology, I suggest a re-evaluation of this unique bear's evolutionary direction and specialized adaptations. I propose the following testable model of *Arctodus'* foraging ecology:

> *Short-faced bears were primarily scavengers of widely dispersed large mammal carcasses and had evolved simultaneously for increased locomotor efficiency and for intimidating other large carnivores. These adaptations allowed Arctodus to forage economically over a large home range and to seek out, procure, and defend carcasses from other large carnivores.*

The model assumes that *Arctodus'* morphology was driven by foraging style (at least in part) and that *Arctodus* was foraging on meat (the omnivore/herbivore niche concept of Emslie and Czaplewski (1985) is rejected based on stable isotope data). Consequently, *Arctodus* must have been either an active predator, a scavenger of carrion, or a combination of both. But if *Arctodus* was engaging in substantial predatory behavior, then I predict that evolution would have shaped this bear quite differently than what we actually find. For instance, if *Arctodus* hunted large, slow moving, pachyderms, then it is difficult to understand why it had evolved a gracile, long-legged postcranial morphology. One would think that such a predator would need to retain a strong, robust build. Conversely, if *Arctodus* preyed on fast-running

ungulates, then its large size is a contradiction, since its mass would have slowed it down and reduced agility. Indeed, a closer scrutiny of *Arctodus*' morphology suggests that short-faced bears had lost features through evolution that would have been beneficial for predatory habits— primarily strength in the limbs, which is necessary either for acceleration or for handling prey.

Furthermore, the presence of other specialized predators on the Beringian landscape precluded much opportunity for another large carnivore to make a living through predation. But the activities of these large predators may have placed more large mammal carcasses on the landscape, thus opening a niche for just such a scavenger— a niche that disappeared with the extinctions of many large prey and their predators at the end of the Pleistocene. Next, I summarize some of the arguments for a scavenging model and demonstrate inadequacies of predatory models (These arguments and evidence for them are examined in more detail in Chapters 2 - 4).

Kurtén (1967a) interpreted *Arctodus*' long-leggedness and slender build as adaptations for fast cursorialism. Most cursorial predators also have powerful limbs designed for acceleration, not just high speed, but that is not what we find in *Arctodus*. Moreover, there is considerable convergence in the morphology of limbs adapted for high speed (without acceleration) and limbs adapted for increased locomotor efficiency. This is because both designs have the same basic goal: to oscillate the limbs through the stride cycle with the least effort (Hildebrand 1985a, b). The main difference between these two limb types is how much dynamic force they can handle, which also is related to an animal's mass. High speed limbs can dissipate more locomotor stresses, but this becomes increasingly difficult in very large animals and that is why they curb speed and sharp turns. I suggest that *Arctodus*' limbs were designed for an energetically efficient and sustainable gait, perhaps a pacing gait, not for high speed or other high-stress activities. Lightening up the rest of the body had similar benefits of increasing locomotor efficiency by reducing the relative mass being propelled by the limbs (see Chapters 2 and 3).

While detrimental for speed and agility, *Arctodus*' extreme size fits well into the scavenging model.[2] First, a larger-bodied animal can cover a larger home range with greater efficiency, enabling it to economically forage for a widely dispersed food resource (Eisenberg 1981, Clutton-Brock and Harvey 1983). Large animals also can eat more at each feeding bout; thus they can take advantage of a large food item when it is available, and they can go longer between feeding, which is advantageous when foraging on widely dispersed and infrequent food items (Houston 1979). Secondly, if *Arctodus* specialized in carcass foraging, but not predation, it would have to procure and defend carcasses from other carnivores, some of which were probably social. Considering the nature and diversity of other Pleistocene carnivores,

[2] Adult short-faced bears were about 700 kg (see subsequent chapters plus Kurtén 1967, Nelson and Madsen 1983; Agenbroad and Mead 1986, Voorhies and Corner 1986, Churcher *et al.* 1993, Richards and Turnbull 1995, Harington 1991, 1996)

and assuming *Arctodus* was a solitary beast, then there should have been considerable evolutionary incentive for *Arctodus* to increase body size in order to intimidate and dominate other carnivores. It may seem contradictory to suggest that *Arctodus* was not strong enough to be an active predator yet was large and strong enough to dominate other carnivores. However, the two concepts can be reconciled: *Arctodus* was so much larger than other carnivores (see Fig. 5 in Chapter 2) that it overwhelmed them with greater absolute strength, even though it was not overly strong for its size and does not appear to have been strong enough to capture and kill the largest Pleistocene herbivores. In fact, I suggest that one of the main reasons *Arctodus* had evolved such a disproportionately huge size was because it sacrificed strength and power in its appendicular skeleton in exchange for enhanced locomotor efficiency.

Compared to both Ursine bears and other Tremarctine bears, the skull of *Arctodus* was shorter in anterior-posterior length, but relatively wider and more robust (Kurtén 1967a). Moreover, the skull was shortened most in the snout and distal tooth row, not the braincase. This configuration necessarily reduces the length of the out-lever of the temporalis and masseter muscles as they close the jaw, especially at the distal teeth, without reducing the size (and thus force) of these muscles. Indeed, the broad parietal region, tall sagittal crest, and wide, robust zygomatic arches of *Arctodus* suggest that its temporalis and masseter muscles were large and developed high in-forces during contraction. Masticatory muscles that develop high in-forces and have short out-levers will deliver especially high out-forces to the teeth (see Section 9 in Chapter 2). Because *Arctodus*' skull was shortened anteriorly, the distal teeth would have experienced the greatest increase in bite strength. Furthermore, *Arctodus* had a long, tall, and posteriorly extended sagittal crest and a tall, broad vertical rami of the mandible. This suggests that *Arctodus* had a well-developed middle and posterior arm of the temporalis muscle, a configuration which imparts its strongest bite at mid-gape (Ewer 1973). Additionally, the P^4 and M_1 are large and conical in *Arctodus*, and it is my opinion that these carnassials did not form a functional shearing edge. (This is a subjective opinion based on personal observations. Illustrations and photos of *Arctodus*' carnassials can be found in Merriam and Stock 1925, Kurtén 1967a, Kurtén and Anderson 1980, Emslie and Czaplewski 1985, Gillette and Madsen 1992, Baryshnikov *et al.* 1994, Richards and Turnbull 1995). Given the strong bite force and lack of shearing ability in the masticatory apparatus of *Arctodus*, I propose that this bear had evolved to crack open the shafts of large mammal long bones using the triangular P^4 and triconid of M_1 as opposing cracking hammers.

Typically, carnivores use anterior cheek teeth to crack large cortical bone, and posterior molars to crush smaller, softer bone (Ewer 1973, Kruuk 1972, Van Valkenburgh 1996). The P^4s of most adult *Arctodus* specimens are heavily worn, especially the protocone and lingual surfaces where they occlude with the triconid of M_1 (personal observation). Clearly, the mouth would be positioned in a somewhat open gape if *Arctodus* was placing wide bones between its anterior teeth in order to crack them, and in

order to crack the bone, *Arctodus* would need to develop a strong bite force at a this gape. I showed above why I think it is reasonable to infer that *Arctodus* did just that based on the arrangement of the temporalis muscle and wear on the carnassials. As a scavenging specialist, bone-cracking abilities may have been an important aspect of *Arctodus'* niche so it could utilize the maximum edible parts of a carcass and extract lipids from the yellow, greasy marrow of long bones.

Speth (1989) and Martin and Martin (1993) have pointed out that a carnivore can not obtain all of its calories from protein (lean meat) for a sustained period, primarily because the animal will eventually exceed the rate at which its liver can metabolize amino acids and detoxify byproducts of protein catabolism (Speth 1989). Carnivores must obtain some calories from lipids or carbohydrates, and lipids provide other critical nutrients, particularly fatty acids. During seasons when the flesh of prey animals is especially lean, carnivores must find supplemental sources of lipids or suffer severe deterioration of their own body condition (Martin and Martin 1993). Carnivores with the ability to open long bones and extract greasy marrow should have a distinct caloric advantage, especially during lean times of limited carcass availability.

Kurtén (1967a: 49) suggested that the wide snout of *Arctodus* was "adaptive for the worrying of prey." As evidence, he points out that the highly carnivorous polar bear has a relatively wide snout. Alternatively, *Arctodus'* wide snout could be a reflection of a highly developed olfactory apparatus that was useful for seeking out carrion. Indeed, the primary hunting strategy of polar bears is to detect seal lairs and breathing holes by smell, and they do considerable scavenging as well (Stirling and Archibald 1977, Stirling *et al.* 1977, Stirling 1988). Furthermore, the prey of polar bears are much smaller than themselves, and the need for a strong, wide snout to kill struggling prey is minimal. F.C. Dean (personal communication, 1995) also has suggested that *Arctodus'* wide skull may have provided for a larger throat passage, which could have been useful for bolting large food items. This is similar to the morphology of spotted hyenas (*Crocuta crocuta*), which swallow large and minimally processed pieces of flesh and bone (Kruuk 1972).

If short-faced bears were large-bodied scavengers capable of stealing carcasses from other large carnivores, and were necessarily aggressive, then it seems unlikely that brown bears could dominate them in direct interference competition. And while brown bears may have been predisposed to feed on animal carcasses, it seems more likely that they would have avoided direct confrontation with a dominant bear. Instead, brown bears would have been doing what they now do best— making use of a variety of dietary resources and only exploiting carrion resources opportunistically. In this hypothesized relationship between brown bears and short-faced bears, it is conceivable that short-faced bears may have competitively excluded brown bears from the New World through until productivity patterns of ecosystems in late Pleistocene Beringia could support both bear species— that is, until the Wisconsinan Glaciation.

The ecological plasticity of brown bears and their ability to hibernate may have been keys to their ultimate survival at the end of the Pleistocene, while *Arctodus*, the highly specialized forager, was no longer able to find a niche in Holocene ecosystems. Most likely, carcass densities on Holocene landscapes fell below levels necessary to sustain minimal viable populations of short-faced bears (addressed in Chapter 4). Since brown bears hibernate to ride out periods of poor food availability, I would speculate that perhaps short-faced bears never had evolved this strategy to survive seasonal dietary bottlenecks. The ability to hibernate and the less specialized foraging requirements of Ursine bears suggests two possible reasons why they continued to persist in the New World, while the Tremarctine bears have all but disappeared.

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CHAPTER II

THE LOCOMOTOR ADAPTATIONS AND ECOMORPHOLOGY OF SHORT-FACED BEARS

PART I: GENERAL EFFECTS OF BODY SIZE AND LIMB MORPHOLOGY ON LOCOMOTOR PERFORMANCE IN LARGE QUADRUPEDAL MAMMALS— *DESIGNS FOR SPEED, ACCELERATION, AND ENDURANCE* [1]

1. INTRODUCTION

The next three chapters re-examine the ecomorphology and locomotor abilities of the extinct short-faced bear (*Arctodus simus*), a formerly widespread indigenous bear of Pleistocene North America. This chapter provides a general review of relevant morphological features that influence performance aspects of locomotion in large quadrupedal mammals, while Chapter 3 is a specific diagnosis of locomotor function in *Arctodus*. In Chapter 4, I model energetic aspects of *Arctodus*' foraging ecology and present a theory for the ecology behind this bear's evolution.

I undertake a fairly lengthy review of locomotion in this chapter for a number of reasons. First, I found that existing interpretations of *Arctodus*' post-cranial morphology are fairly cursory, speculative, and draw on inaccurate concepts about locomotor dynamics. To rectify this, it seemed important to synthesize information relating to the mechanics and physiology of locomotion relevant to the *Arctodus* question— namely the effects of very large body size and long gracile legs. However, in this chapter I discuss *Arctodus* very little. Instead, I lay down general arguments for locomotor adaptation, which allows me to be more direct and concise in Chapter 3; rather than cluttering that chapter's discussion of *Arctodus* with digressions and explanations of biomechanics and physiology, I can refer the reader back to concepts established here. I also feel that this elaboration is necessary because I will make conclusions about *Arctodus* which are not always intuitive and which are contrary to current beliefs about this unusual bear's behavior. Finally, this chapter's review may provide other vertebrate paleontologists with a convenient synthesis of some current concepts regarding locomotion from the perspective of physiologists and anatomists.

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[1] This chapter was written as the first part of a three-part monograph on the locomotor adaptations and ecomorphology of short-faced. Chapters 3 and 4 constitute the other two parts

Preliminary Considerations

a. Current Ecological Models and the Hypotheses Being Tested

Chapters III and IV contain more thorough discussions of the *Arctodus* problem, but I will briefly introduce the issues here, so the reader understands the direction I am heading (also see Chapter I and Matheus 1995). Kurtén (1967a) was the first to seriously address the functional implications of *Arctodus*' morphology, and he concluded that this bear was a fast, cursorial super-predator that had evolved as a specialized hunter of North America's Pleistocene megaherbivores. Kurtén's conclusions regarding *Arctodus*' predatory behavior and cursorialism were based on the fact that this huge bear had a powerful, robust cranium, which Kurtén argued was adaptive for prey capture, and a gracile, long-legged postcranial design, which Kurtén thought was adaptive for speed and cursorial pursuit. The premise that *Arctodus* was at least carnivorous and probably an active predator has been widely accepted with little qualification from Kurtén's original model (Harington 1973, 1977, 1996; Kurtén and Anderson 1980; Agenbroad and Mead 1986; Agenbroad 1990; Voorhies and Corner 1982, 1986; Guthrie 1988, 1990a; Gillette and Madsen 1992; Churcher *et al.* 1993; Baryshnikov *et al.* 1994; Richards and Turnbull 1995; Richards *et al.* 1996). However, it is a premise I will try to refute.

Emslie and Czaplewski (1985) have voiced the only dissent regarding *Arctodus*' carnivorous habits. These authors argue that short-faced bears were not cursorially adapted and must have been herbivorous because, in their estimate, such a large carnivore would have had to procure an unrealistic amount of animal biomass (meat) to achieve its energetic requirements. They formulated the latter argument based on data in Eisenberg (1981), who summarized patterns relating body size to trophic position and showed that no modern terrestrial carnivore approaches the size of *Arctodus*.

Using stable isotopes, I rejected Emslie and Czaplewski's hypothesis by showing that short-faced bears were highly carnivorous (Chapter 1, Matheus 1994a, 1995). In those works I also laid down preliminary arguments showing that *Arctodus* was not built to be an effective predator because it most likely was incapable of accelerating rapidly and generating high speeds (or at least not maneuvering at high speeds)— all traits that are necessary to one degree or another for essentially all modes of prey capture. As an alternative hypothesis, I suggested that this bear showed the traits predicted for an animal that had evolved to locomote with great economy and for sustained travel. Thus, I proposed that *Arctodus* mainly functioned as a wide-ranging scavenging specialist that had evolved to efficiently cover a very large home range in order to seek out, procure, and defend megafaunal carcasses from other large carnivores.

In this chapter and the next two, I will follow up on this hypothesis by trying to show in more detail why it is unlikely that *Arctodus* was much of a predator. Baryshnikov *et al.* (1994) also have

suggested that *Arctodus* may have had scavenging habits (as do most carnivores). In addition, Voorhies and Corner (1986), Guthrie (1988, 1990a), Agenbroad (1990), and Harington (1996) alluded to the possibility. However, none of these authors has suggested that scavenging was *Arctodus' primary occupation* and they assert that this bear was still an active, capable predator. In contrast, I will use the evidence presented in these three chapters to show that *Arctodus* had evolved specifically as a scavenger, and, while I do not deny that *Arctodus* may have occasionally killed its own prey when the opportunity arose, it simply appears that this behavior was not the driving force that shaped *Arctodus'* morphology—but scavenging was.

b. Primer on Arctodus' Morphology

Knowing that *Arctodus* was carnivorous, the key to reconstructing its foraging ecology lies in diagnosing the adaptive significance of its highly derived morphology. Again, this subject will be addressed in detail in Chapter 3; only a summary of *Arctodus'* morphology is provided here for orientation. Also, these chapters only will address specific details of post-cranial adaptations; while *Arctodus'* cranial morphology provides additional clues into its foraging behavior, I am dealing with that subject in a separate manuscript (in prep). (My hypothesis regarding *Arctodus'* cranial features are presented in Matheus 1995 and in Chapter 4)

Short-faced bears were extremely large, even for bears (Figs. 4 and 5), and various attempts have been made to estimate the body weight of individual specimens (Kurtén 1967a; Nelson and Madsen 1983; Agenbroad and Mead 1986; Voorhies and Corner 1986; Churcher *et al.* 1993; Richards and Turnbull 1995; Harington 1991, 1996). Nearly all of these estimates were calculated using allometric equations relating long bone cross-sectional area to body mass, whereas the remainder are best guesses that rely on comparisons to samples whose weights were estimated from long bone cross-sectional area. Generally, these authors estimated that males were around 600 - 700 kg and perhaps reached 800 kg. Voorhies and Corner (1986) even suggested that large males may have topped 1000 kg. Kurtén (1967a) showed that sexual dimorphism was pronounced, as it is in other bears, and is on the order of 15 - 25 %, placing females around 450 - 600 kg. If Voorhies and Corner's extreme estimate (1000 kg for males) is correct, then some females may have even reached nearly 750 kg. Considering *Arctodus'* gracile build, I think that Voorhies and Corner's estimates are too extreme. Indeed, the bulk of this chapter will discuss the ramifications of such large size, and I will frequently reiterate that body mass and both static and dynamic forces of support increase with body size at a greater rate than the support capability of long bones. This should be a strong clue that such a large animal like *Arctodus* with gracile limbs must have been very lean. Furthermore, Voorhies and Corner do not explain how they derived their estimate of 1000 kg for large males in their 1986 paper, but based on the their 1982 article it seems that they arrived at this value

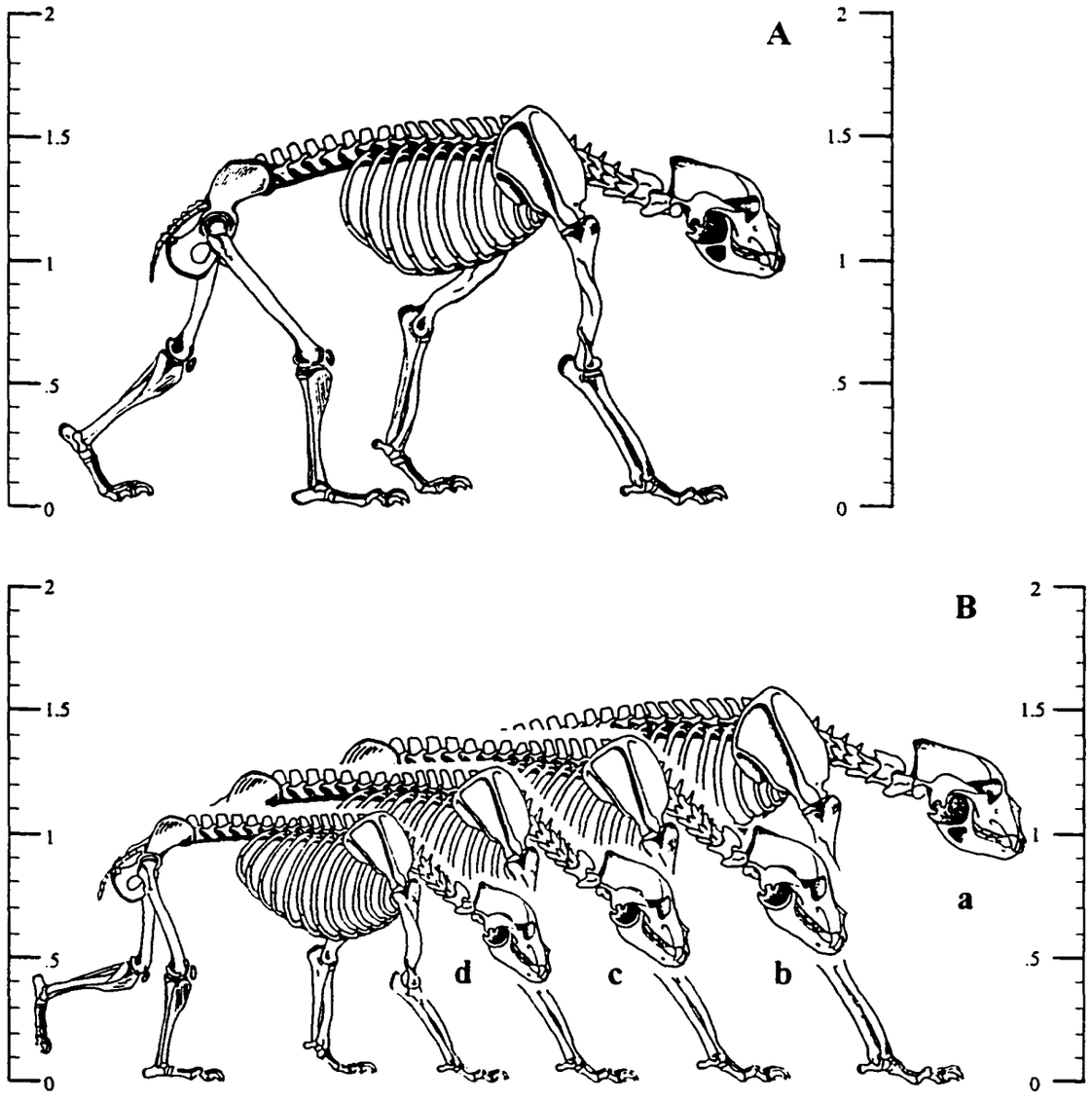

FIGURE 4. A) Reconstruction of the short-faced bear's skeletal conformation. B) Size comparison between short-faced bears and various brown bear morphs: *a* = large male short-faced bear, *b* = largest size attained by coastal brown bears today (could also represent the largest polar bear), *c* = large male brown bear typical for eastern Beringia during the Pleistocene (also approximate size of a large male modern coastal brown bear), *d* = large male grizzly from modern interior Alaska (units in meters)(original illustrations by author).

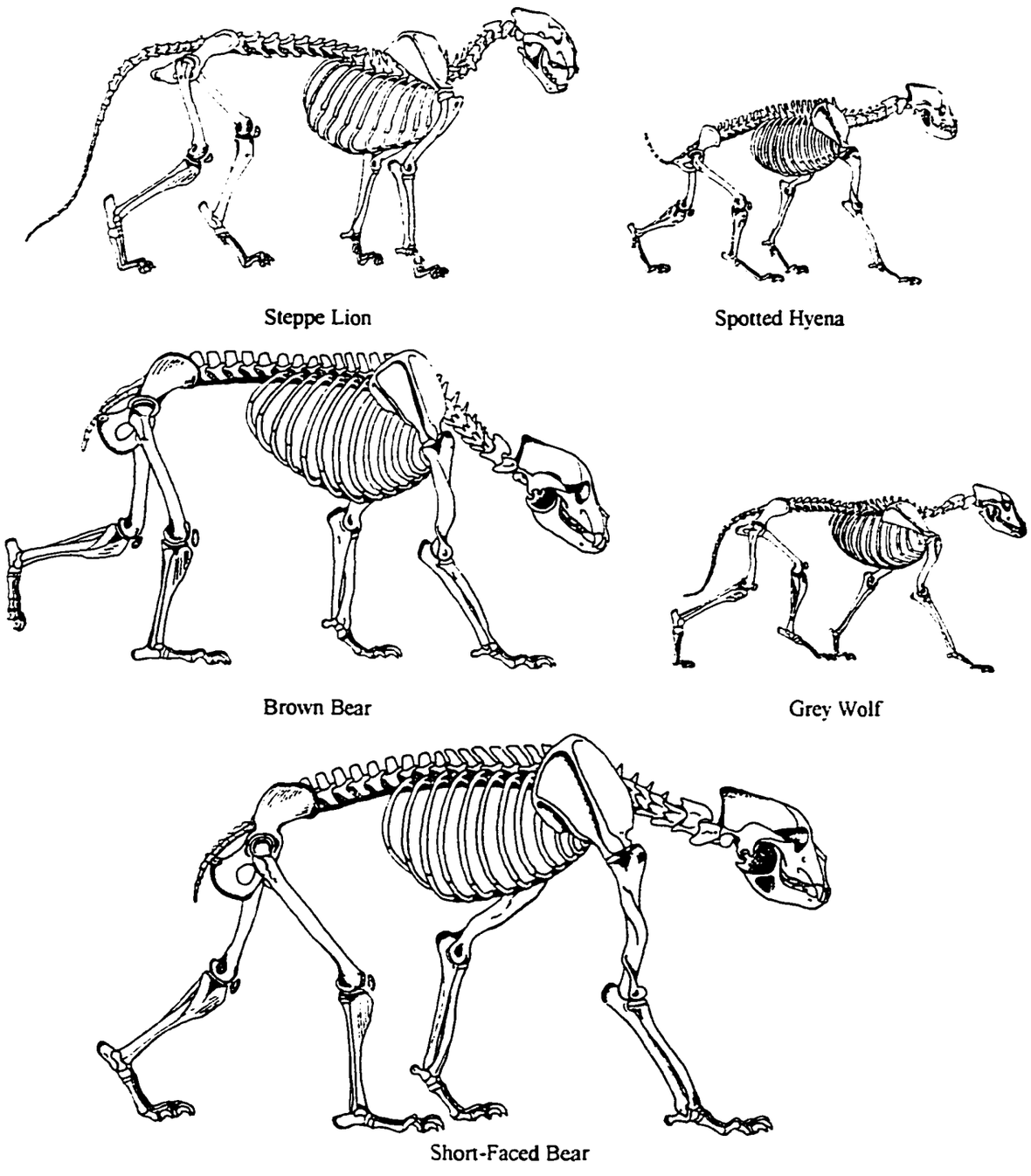

FIGURE 5. Body size and skeletal conformation of short-faced bears and other carnivores discussed in Chapters 2 - 4. All body sizes adjusted to depict adult males in Pleistocene east Beringia, except hyena, which did not occupy Beringia (original illustrations by author).

simply by their impression with how big *Arctodus* long bones are compared to those of modern black bears (*Ursus americanus*).

Even if one accepts a conservative estimate of 500 kg and 600 kg for an average female and male short-faced bear, respectively, this means that an average individual was nearly as massive as a domestic horse and two to three times the mass of a modern, non-coastal grizzly bear (*Ursus arctos horribilis*). Figure 4b compares the skeletal size of *Arctodus* (*a*) to three morphs of male brown bears: the largest known modern, male, brown bear (which could also represent the largest known polar bear) (*b*); a very large modern, male, brown bear from coastal Alaska or Kamchatka (also the size of a typical large brown bear from interior Alaska during the Pleistocene) (*c*), and; a large, modern, male brown bear typical of interior Alaska, the contiguous 48 United States, Europe, and interior Russia (*d*). Figure 5 compares the size of *Arctodus* to other carnivores that will be discussed in this and subsequent chapters. A primary thesis throughout these chapters will be that *Arctodus*' enormous size is one key to understanding its locomotor abilities and foraging behavior and that *Arctodus* was too large to be an effective predator.

Comparisons to other bears, however, can be misleading because *Arctodus* was not built like more familiar modern bears. In contrast to the stereotypical impression of a bear's morphology, *Arctodus* had a very light build, with a laterally compressed but deep thoracic cavity, and limb bones that were very long, gracile, and lacked much of the characteristic bowing and toe-in posture of ursine bears (Chapter 3, Merriam and Stock 1925, Kurtén 1967a). I discuss these traits in detail in the next chapter, where I also will show that, contrary to other portrayals (Kurtén 1967a, Baryshnikov *et al.* 1994), *Arctodus*' front legs were especially long compared to the hind legs and that it had a fairly short back. This configuration gave *Arctodus* a high-shouldered, sloped-back appearance, which is significant for diagnosing its gait and locomotor adaptations. The paws (metapodials and phalanges) also were characteristically long and slender in *Arctodus* and more elongated along the central (third and forth) digits, compared to Ursine bears (Kurtén 1967a). This means that *Arctodus*' paws were more symmetrical than Ursine bears, whose feet have axes aligned with the most lateral (fifth) digit (Kurtén 1967a). Also, the first digit (hallux) of *Arctodus* was positioned more closely against and parallel to the others four digits, compared to Ursine bears (i.e., it had less lateral splaying)(Kurtén 1967a). Considering these traits, *Arctodus*' large size, and its gracile build, short-faced bears must have appeared incredibly tall and lanky compared to extant bears.

More details on *Arctodus*' morphology follow in the next chapter, but here I want to make the point that *Arctodus*' morphology is quite derived from other bears, both modern and fossil. In this regard, I strongly disagree with the conclusions of Baryshnikov *et al.* (1994:350) (who argued that *Arctodus* had a propensity for scavenging) when they stated, "These limbs and locomotion are *satisfactory* for a scavenger," implying that there would be little, specific selective pressure on the locomotor morphology of a scavenging bear (emphasis on "satisfactory" is mine). The image of *Arctodus* as an unspecialized

forager that made a living on the "leftovers" of other, more highly adapted, carnivores and the idea that scavengers are necessarily generalists, are two myths that I will try to dispel. Baryshnikov *et al.'s* (1994) interpretation seems especially inappropriate for a bear which had evolved a morphology so divergent from other bears.

c. Limbs are Compromises

Performance aspects of quadrupedal locomotion, such as top speed, acceleration, endurance, and maneuverability, depend on limb conformation in conjunction with other body proportions, as well as overall body size and metabolic limitations. Any analysis of limb design also must consider that limbs do not evolve solely for locomotion, but are employed for non-locomotor functions as well.[2] Even within the realm of locomotion, limb design is a tradeoff between competing demands: it is practically an axiom amongst morphologists that limbs designed for high velocity can not simultaneously function for high power output (Hildebrand 1995:445), and sometimes it is difficult to make *a priori* determinations about the precise selective pressures driving limb morphology in an extinct species. Phylogeny and evolutionary time also place constraints on the direction and rate of limb evolution. It is unrealistic, for instance, to expect a species with cheetah-like proportions and running abilities will arise within an ursid lineage in only one million years (yet this is almost what has been suggested for *Arctodus*). For the same reason, one should not expect animals to be perfectly adapted for a particular niche at any given time during their evolution— but this does not mean that they are not being shaped by strong selective pressures. Therefore, multiple demands on limbs, as well as phylogeny and evolutionary time frames, can confound attempts to decipher the precise locomotor habits of an extinct and unique animal such as the short-faced bear, which has left few other clues about its niche.

d. The Comparative Approach and Layout of this Chapter

The most intuitive starting point in deciphering an extinct species' locomotor abilities is to make comparisons with extant animals. However, I think that there are no good analogs for *Arctodus*. What's more, the comparisons which have been made only involve comparisons with other species of Carnivora (e.g., Kurtén 1967a, Emslie and Czaplewski 1985, Agenbroad and Mead 1986, Baryshnikov *et al.* 1994). It is my contention that this perspective has sent researchers down the wrong path towards understanding this bear's life, because short-faced bears were not built like other Carnivora and they were not simply scaled-up bears (discussed in detail in Chapter 3). In fact, for some morphological features, better analogs probably can be found from the ranks of other very large, long-legged mammals outside of the Carnivora.

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[2] Throughout this thesis, the term "designed for" is used as an efficient euphemism with the meaning "evolved under selective pressure for."

It is because of this problem of analogs, a process which lends itself to oversimplified and misleading comparisons, that I am approaching the *Arctodus* problem mainly using first principles of locomotor dynamics. That also is why I will spend so much time discussing first principles for the remainder of this chapter. If one analyzes *Arctodus* without any *a priori* assumptions about the way it moved, but instead dissect its parts and proportions to determine the functions they are optimized for, then a different picture of this bear emerges.

The remainder of this chapter is divided into nine sections that discuss facets of locomotion relevant to the *Arctodus* problem. The first four sections (Sections 2-5) mainly define terms and introduce concepts which I refer to repeatedly, including discussions on cursorialism, gait terminology, and scaling in quadrupedal mammals. Then, I review current concepts on the energetics of locomotion (Section 6), where the importance of body size becomes apparent. Body size also is the main theme in the next two sections (7 and 8), which examine the ways that body size influences muscle performance and bone loading— two critical issues for very large mammals. Finally, I discuss limb mechanics from the classic perspective of lever systems (Section 9) and kinematics (Section 10). These last two sections mainly consider concepts of mechanical advantage and the effects of limb mass on locomotor performance, and it is here that I distinguish ways that mammals are built for different types of locomotor abilities such as acceleration, endurance, and high speeds. Because of the two prominent traits in *Arctodus*— its extraordinarily large body size and long, gracile legs — the effects of body size and limb dimensions on locomotor performance will be dominant themes throughout these discussions. In this chapter and the next, I will try to show that large size and long, gracile limbs would have afforded *Arctodus* certain locomotor advantages, such as increased stride length and economy of travel, while limiting it in other ways— namely the ability to accelerate and maneuver at high speeds.

2. Definitions

The following terms will be used throughout this and the next two chapters, some frequently and some in passing. They are defined or summarized here for quick reference, but important conceptual terms also are discussed in the text.

acceleration (a) = v / t (general linear); $a = d v / d t$ (instantaneous); $a = \Delta v / \Delta t$ (average); change in velocity per unit time usually measured in m / s^2; as with velocity terms, the acceleration of limbs or individual body parts is distinct from whole body acceleration (change in ground speed).

angular acceleration (α) = $\omega \quad t$ (general); $\alpha = d \omega$ $d t$ (instantaneous); $\alpha = \Delta \omega \quad \Delta t$ (average); curvilinear equivalent of linear acceleration.

angular momentum (L) = $I \cdot \omega$; the curvilinear equivalent of linear momentum.

angular velocity (ω) = $L \quad I$; ω = d L d I (instantaneous); ω = ΔL ΔI (average); curvilinear equivalent of linear velocity

cost coefficient of locomotion rate of energy consumption by each kg of body mass during steady state locomotion; does not depend on distance traveled but purely on mass-specific rate of consumption; compare to *cost of transport*.

cost of transport amount of metabolic energy consumed per kg of body mass per km traveled during locomotion; also called the *mass specific cost of transport*; not the same as the *cost coefficient of locomotion*.

courser (*cursorial*) an animal that has evolved substantial musculoskeletal features which reduce the effort required to swing the limbs and propel the body; includes animals adapted as such for either sustained locomotion or higher sustainable speeds, but these adaptations do not necessarily increase acceleration (that is a function of power output).

economy of effort similar to efficiency, it is a term that emphasizes the amount of effort required for a given task; increased economy may be achieved by increasing energetic efficiency or by reducing the absolute amount of work necessary for a task.

endurance measure of an animal's ability to sustain a given speed or activity; endurance is increased by increasing economy of effort.

force (F) = $m \cdot a$; expressed in kg/cm ^{2}or Newtons, force is the quantity of push or pull that drives (accelerates) or slows (decelerates) motion in a unit of mass; forces applied to solid surfaces are *called loads*; quantity of force generated by a muscle is a function of its cross-sectional area.

gait a regular and repeated pattern of footfalls used by an animal during locomotion.

inertia (m) measured as mass; tendency of an object to remain at rest or in uniform motion (constant velocity and direction) unless acted upon by a force; weight is gravitational inertia, or $m \cdot g$.

in-lever moment arm on the side of a fulcrum (joint) receiving an in-force; see *moment arm*.

kinetic energy (E_k) = $^1/_2 m \cdot v^2$ (rectilinear); E_k = $^1/_2 I \cdot \omega^2$ (curvilinear); energy of motion; may be converted to potential energy (E_p) or stored as elastic strain energy in tendons; energy is used to perform work.

limb velocity velocity of a whole limb or limb part relative to the body's center of mass.

load (*and loading*) any force applied to a solid object such as bone, muscle, or tendon.

locomotor efficiency ratio of the energy consumed during locomotion versus an output variable such as the amount of work performed or force generated.

mechanical advantage in-lever:oulever ratio in a lever or limb; high mechanical advantage gives a limb more torque but decreases rotational velocity.

moment see torque

moment arm or *lever arm* lengths of the levers (*in-levers* and *out-levers*), or arms, in a lever system; the length of a moment arm times a force is called a *moment*, *turning force*, or *torque*

moment of inertia (I) = $m \cdot D^2$; the curvilinear equivalent of inertia; I is a function of mass and the length of its rotational axis.

momentum (M) = $m \cdot v$; a moving mass' capacity to resist a change in velocity or overcome resistance.

out-lever moment arm on the side of a fulcrum (joint) delivering an out-force; see *moment arm*.

power (P) = $F \cdot v$ or P = W t , the rate of force application or the time over which a unit of work is performed; in a muscle, power is a function of the force applied times the rate of contraction. Power generation is directly related to limb/muscle acceleration. Physiologists measure *metabolic power* as the rate of oxygen consumption.

radius of gyration (D) length of a rotational axis; in a pendulum it is the distance from the pivot point to the center of oscillation.

run any gait where each foot is on the ground less than half the stride cycle and there is an unsupported (aerial) phase.

safety factor (*safety margin*) ratio between a bone's normal strain and yield strain.

speed (*ground speed*) average forward velocity of an animal's center of mass relative to the environment; calculated as stride rate x stride length or as step length ÷ by time of foot contact with the ground (and by other means).

step length distance the body moves forward while a single foot is on the ground during a stride.

strain physical deformation in a solid material such as bone, muscle, or tendon during the application of a force (i.e., during loading).

strength (of bone) ability to deform under stress without breakage or permanent deformation; or the ability to dissipate strain.

strength (of muscle) amount of work a muscle can perform; is not equivalent to power.

stress force transmitted within a bone due to loading.

stride cycle cycle of motion during which each foot has completed one footfall.

stride length distance the body moves forward during one complete stride cycle.

stride sequence order of individual footfalls during a stride cycle.

torque, or turning force (τ) $= I \cdot \alpha$; curvilinear equivalent of force; in a lever system a torque is called a ***moment*** and is the product of a force times a moment arm.

velocity (v) $= d \; t$ (general, linear), $v = \mathrm{d}\, d \;\; \mathrm{d}\, t$ (instantaneous), $v = \Delta d \;\; \Delta t$ (average); velocities are vectors so they have both magnitude and direction; as with acceleration, the velocity of a limb or body part is distinguished from the whole body velocity, or ground speed.

walk any gait where each foot is on the ground more than half the stride cycle and there is no unsupported (aerial) phase.

work (W) $= F \cdot d$; the distance over which a unit of force is applied; in a muscle, work is roughly a function of volume; work is not always an informative concept in locomotion because it is not time dependent and force can be exerted without performing work if no change in position (distance) occurs.

3. Confusion Regarding Cursorialism

When Kurtén (1967a) assessed *Arctodus* as a fast, cursorial predator, he followed common misconceptions about what cursorialism is and is not. Cursorialism is not strictly, nor principally, about adaptations for running at high speeds. That is merely one form of cursorialism, and assuming that all coursers are built for speed (a somewhat misused term, itself) gets away from the heart of what cursorial adaptations are all about: musculoskeletal and physiological modifications that increase the efficiency of energy expenditure (i.e., economy) while swinging the limbs and propelling the body through a stride sequence. This definition most closely follows Hildebrand (1985a, 1995), who considers coursers to be animals that are structurally modified to benefit speed *or* endurance; they travel fast *or* far and are distinguished from non-cursorial animals, which do not show structural modification for specialized locomotion and who rely principally on walking gaits (the latter are termed "amblers").

Some authors (for example, Alexander and Jayes 1983) prefer Jenkins' (1971) definition of cursorialism in mammals, which is based more on size and posture than function. According to Jenkins, cursorial mammals stand and run with their legs less bent, with the femur and humerus positioned nearly vertically, and they swing their limbs with little deviation from the sagittal plane. By this definition, nearly all mammals greater than 10 kg are cursorial and no very small mammals would be considered

cursorial. The strength of Jenkins' definition is that it does not use speed or running ability as criteria for cursorialism, but its dependence on mass is misleading. Small mammals do not necessarily move any less "cursorially" than large mammals, but because the stresses of locomotion and support scale in their favor, small animals do not need to make such severe skeletal modifications (see later sections). Furthermore, Jenkins' definition is too general for my purposes, since I am discussing finer-scale details of cursorialism across a narrow range of taxa.

Taylor (1989), who considered cursorialism specifically in carnivores, distinguished three types of coursers: 1) those designed for prolonged, moderate speed travel, usually using a trot, but which seldom use high speeds (e.g., hyenids and some canids), 2) those that depend on a combination of speed and stamina for higher speed pursuit (e.g., African hunting dogs, *Lycaon pictus*), and 3) those that are built for extreme acceleration and high, but unsustainable, speed (e.g., large felids). Perhaps these are more appropriately called categories of running, rather than cursorialism, but Taylor acknowledges the critical distinctions between high speed, acceleration, and endurance, and the fact that coursers make tradeoffs among these three (a point I will emphasize throughout this chapter).

Frequently, the distinction between coursers adapted for sustained long range locomotion versus locomotion at high speeds (running) is a matter of ecology: animals adapted for sustained travel often migrate to follow seasonally available resources and/or are constantly on the move to forage, while those adapted for acceleration or high speeds absolutely rely on running to capture food or to escape predation. The important difference between the two categories often comes down to this: while long distance coursers *can* run, they often do not depend on it, and frequently they lack good running skills. The camel, for example, is the quintessential long range courser, and while it *can* run, it accelerates and maneuvers (at high speeds) very poorly.

Cursorial adaptations are most pronounced in the appendicular skeleton and principally involve modifications that affect the relative lengths of limb segments and the distribution of weight along the limbs (see section on kinematics). Generally cursorial modifications do not directly increase top speed. *The main effect of cursorial modifications is that they allow a given speed to be maintained for a longer period*— by decreasing the energy required to swing the limbs, the muscles fatigue more slowly. Cheetahs, for example, are less cursorially modified than the gazelles they chase. Yet, cheetahs achieve the highest speeds amongst quadrupeds and their success at hunting is based on their ability to accelerate faster than their prey (after stalking within range). Without doubt, cursorial adaptations are beneficial to sprinters, such as the cheetah, but mainly because they allow them to sustain their speeds for longer periods, and I will be showing that some cursorial adaptations improve acceleration, while others detract from it. Without its advanced cursorial features, a cheetah would perform no better than a diminutive lion. With cursorial modifications, the cheetah still can only sustain its extraordinary speeds for up to about ½

km (Schaller 1969). After this distance, the cheetah is exhausted and has accrued a large lactic acid debt, whereas the more cursorial gazelle continues to run for many kilometers without fatigue.

These examples illustrate how cursorialism is a relative term. Some authors even go to the extreme by considering only ungulates to be fully cursorial, referring to most carnivores, including the cheetah, as "sub-cursorial" (for example, Coombs 1978). Ungulates truly are the most cursorially adapted quadrupeds, but cheetahs also show advanced cursorial modifications, especially compared to other felids, which are all much more cursorial than brown bears, for instance. But this type of comparison (ungulates versus large predators) shows the fallacy of defining cursorialism as a simple gradational scale. There are distinct types of coursers, ranging from high speed sprinters to long-range migrators and comparisons of degree only should be made within categories. When Kurtén (1967a) surmised that *Arctodus* was cursorially adapted, he was probably correct, but I will be showing why I think he was incorrect when he assumed this implied *Arctodus* was adapted for high speed running and sprinting.

4. Quadrupedal Gaits

I provide the following review of gait terminology and classification because I will argue in Chapter 3 that *Arctodus* would have relied heavily on a very particular gait— the pace— and that this fact reveals a lot about *Arctodus*' behavior.

Quadrupedal locomotion involves the concerted oscillation of four limbs through a repeated stride sequence, or *gait*. A gait is the regular and repeated pattern of footfalls used by an animal during locomotion. Gait selection varies with speed of travel and can differ considerably among species. Over the past few decades, Hildebrand has done the most, by far, to categorize animal gaits and provide a formalized terminology to describe gait patterns, and my definitions below mostly follow his (Hildebrand 1959, 1976, 1977, 1980, 1985a, 1995; but also see Muybridge 1899, and Gray 1968). There are deviations in the literature from Hildebrand's terminology, particularly in the use of the terms *walk* and *run*, but the discrepancies are not of critical importance here. In this chapter, I am most interested in the strategies and limitations of gait selection in animals of a certain size or shape, and what this implies about their behavioral ecology.

In gait terminology, a *stride sequence* refers to the order of footfalls, and one *stride cycle* is completed after each foot has completed one stride. *Stride length* is the distance the body moves over the ground during one stride cycle. I also will refer to *step length*, which is the distance the body moves while a single foot is on the ground (Gray 1968). *Ground speed* refers to an animal's whole body velocity and is distinct from the velocity of limbs or limb segments. Ground speed is a product of stride length times

stride rate or can it be calculated as a single foot's step length divided by the time of its contact with the ground. An animal increases ground speed by increasing either stride rate or stride (step) length, but mostly the latter (Heglund *et al.* 1974).

A *walk* is defined as a gait whereby each foot is on the ground for more than half the time of one stride cycle, and during a walk there are no unsupported (aerial) phases during which all feet are off the ground. Viewed another way, there are never fewer than two feet on the ground in a walk. When an animal *runs*, each foot contacts the ground for less than half the stride cycle, and there is at least one aerial phase. Numerous walking and running gaits have been described and some can be used either during a walk or a run, the distinction being whether or not there is an aerial phase. Because of this confusion, the terms "walking" and "running" can be imprecise and they do not describe specific footfall patterns. For this, the convention is to use terms such as "singlefoot," "trot," "gallop," and "pace."

All the animals I will discuss use a *singlefoot* when walking at slow speeds (the singlefoot is not limited to slow speeds as it is the "running" gait of elephants, and horses that "rack" (Hildebrand 1985a)). During the *walking singlefoot*, each foot is placed on the ground one at a time and consecutive footfalls are evenly spaced in time— neither front nor hind feet move in couplets. Furthermore, during slow walks most quadrupeds use a *lateral singlefoot*, whereby each fore footfall follows the hind footfall on the same side of the body. The lateral singlefoot is a very stable gait, and animals can make the transition from a lateral singlefoot to faster gaits smoothly. The *diagonal singlefoot* is even more stable, but it is used only by primates and wide-bodied quadrupeds with short legs relative to their body length, such as suids and hippopotami (Hildebrand 1976). Other quadrupeds with longer legs apparently avoid the diagonal singlefoot because diagonal pairs of front and hind feet would cause interference with each other during the stride (Hildebrand 1976, Dagg 1979). Furthermore, wide-bodied quadrupeds would have difficulty balancing on lateral legs and perhaps they retain short legs in order to use a diagonal sequence walk without leg interference. Phyologenetically, it appears that the lateral singlefoot is a primitive gait that gave rise to many other footfall sequences (Hildebrand 1976).

The *trot* is a diagonal gait whereby two legs on opposite sides of the body swing as a pair and ipsilateral legs are considered to be "out of phase." The trot may be used either as a fast walk or a slow run, but more commonly the latter. It is the most frequently used moderate-speed gait for medium to large quadrupeds, and it is favored by large carnivores (Hildebrand 1976). Because ipsilateral legs are out of phase in the trot (one swings forward while the other swings rearward) interference between front and hind feet must be resolved. As a result, some quadrupeds trot with their bodies "cocked" laterally a few degrees so that front and hind feet are swung either to the inside or outside of each other (personal observation). Because of interference problems, small feet appear to be an asset for trotters— big-footed bears, for instance, rarely trot (but for more reasons than just foot size— see below).

A major determinant of trotting ability appears to be the relative proportions of the limbs and back. Animals with front legs considerably longer than their hind limbs and with short, sloping backs either never or seldom trot at moderate speeds. Examples include spotted hyenas, giraffes, polar bears, brown bears, and camels (personal observation; Pennycuick 1975, 1979; Hildebrand 1976; Dagg 1979). I suggest two reasons for this. First, the two in-phase legs on opposite sides of the body would have very disparate natural stride lengths, producing an uneven and inefficient trot (pacers (see below) overcome this, whereas trotters cannot, by flexing the trunk laterally). Second, and more important, if an animal with a short-back were to use a trot, there would be too much overlap between the paths of the front and rear legs on each side of the body, causing either excessive interference or a much reduced stride length. It has also been observed that quadrupeds specializing in long range migrations, such as blue wildebeest (*Connochaetes taurinus*), may bypass the trot and go directly from a walking singlefoot to a canter, even though they are capable of trotting (Pennycuick 1975). Later I will show specifically why short strides lead to inefficient locomotion. In the next chapter, I will show that short-faced bears had short, sloping backs and were tall in the shoulder, and that they probably were incapable of trotting.

Quadrupeds that cannot trot typically will use the *pace* for moderate speed travel. In contrast to the trot, the pace is a lateral gait whereby the front and hind legs on each side of the body swing in phase. Like the trot, the pace can be used as a walk or a run. Typical pacers include camellids (all species), giraffids (*Giraffa spp.*, *Okapi johnstoni*), saiga antelope (*Saiga tatarica*), hyenas (*Crocuta crocuta* and *Hyena spp.*), and long legged dog breeds (*Canis familiaris*). Most large carnivores, including bears, occasionally pace, (personal observation, Hildebrand 1976, Dagg 1979), but in the next chapter, I will show why short-faced bears seem to have evolved specifically as pacers. Pacing eliminates the issue of foot interference, so it is used by animals with legs that are long relative to the length of their back. But the greatest assets of pacing seem to be that it allow for longer strides and lets an animal use trunk muscles to assist in extending and flexing the limbs (Dagg 1979). Long strides increase locomotor efficiency, the mechanics of which will be discussed in Section 6. By using trunk muscles, pacers spread the work of locomotion over more muscle groups and each fatigues less quickly. I (unpublished data) have observed that during training runs in the early season, sled dogs that normally trot will revert to a pace when they become fatigued, apparently because pacing relieves tired leg muscles. The same pattern can arise in sled dogs that receive minimal rest between hard workouts or in older dogs (personal observation).

Gaits like the pace, which use laterally supported legs, are inherently less stable than diagonal gaits (Dagg 1979, Hildebrand 1985a), and to keep balanced a pacing animal must place its feet more directly under the body's mass. Wide feet, such as in camels, and giraffes, also help to maintain stability during a pace. Because of the pace's instability, it is commonly believed that only animals inhabiting open country with a smooth substrate utilize the pace (Hildebrand 1977). However, Dagg (1979) showed that

there can be a phylogenetic propensity to pace, regardless of habitat. She noted that all camellids, including lamoids, have a tendency to pace even when living in rough, mountainous terrain. Although there is a phylogenetic component to gait selection, there seem to be two functional reasons why the pace has evolved in large mammals: 1) to accommodate long legs or legs with disproportionate lengths (e.g., giraffids and hyenas), or 2) to increase the efficiency of prolonged travel at moderate speeds (e.g., some camellids and saiga). Large carnivores tend to use lateral gaits to a large extent (Dagg 1979), but few other than hyenas pace for long distances. These arguments do not mean that all efficient long-range coursers will be pacers. Caribou, for instance, do not pace but are efficient long-range trotters. In caribou, trotting may be necessary because tundra ground is very broken and requires a more stable gait.

There seems to be a general belief that large bears (e.g., brown bears and polar bears (*Ursus maritimus*)) are pacers. Based on my own observations of live and videotaped bears (unpublished data), I believe this is a false notion. Ambling (walking) bears almost exclusively use a lateral singlefoot, like all other large carnivores. Occasionally, a walking bear will pace, but this behavior seems to be involved with intraspecific demonstrations. Data on gait selection in Dagg (1979) and Hildebrand (1976) also indicate that bears rarely pace, and I believe the perceptions that bears pace has arisen because the lateral singlefoot has a footfall pattern superficially resembling a pace. In the lateral singlefoot, the left hind leg is placed down, followed by the left front leg; then the right hind leg is placed down, followed by the right front leg. The legs are also lifted in this order, which can give the appearance that the two legs on a side are moving as a pair, but they do not. Especially misleading is the fact that a photograph taken at the right moment during footfalls can make a bear using a lateral singlefoot appear to be pacing.

The few times I have observed brown bears pacing has been mostly when they are making the transition from a galloping gait (see below) down to a walking gate. In these cases, the pace is done at moderate speeds (slow run) and only for a brief transitional period. Bears using this running pace look quite awkward because their hind limbs are too long for the front limbs, causing them to swing their hips laterally back and forth for each stride. Therefore, this gait probably is relatively inefficient and may be one of the reasons why bears (like other amblers) rarely use intermediate speeds. I (unpublished data) also have observed that Polar bears, which have conspicuously high hips compared to brown bears, will occasionally trot but rarely pace. This seems especially true of smaller individuals, mainly females, where the tall hind quarters are accentuated. Polar bears, with their high back ends, actually adopt a trot similar to a canids (personal observation, but also see Hildebrand 1976). This pattern is important because it shows how tall hind limbs promote trotting over pacing in bears. The running style of bears is discussed more below, and in the next chapter I will explain why it seems that short-faced bears, with their tall shoulders and short hind-quarters, would have been incapable of trotting and relied heavily on pacing.

The *gallop* and the *bound* are the two fast running gaits used by the animals discussed in

subsequent sections of this chapter. During both of these gaits, the two front and two hind feet each travel as pairs and are called couplets. In each couplet, the feet usually are somewhat out of phase with each other, in which case the foot leading in space is called the "leading" foot, while the other is the "trailing" foot. Although trailing in its flight path, the trailing foot usually hits the ground before the leading foot (as Hildebrand (1976) pointed out, the trailing foot trails in space, not time).

In the *bound*, the spacing (in space and time) between the leading and trailing feet is so small that each couplet appears to move with both feet virtually in phase. A bounding animal essentially makes two jumps— one by the hind feet, then one by the front feet. In small mammals with very flexible backs, like weasels, the bound resembles a slinking motion. In the *half bound*, there is no lead in the hind feet, but there can be considerable lead in the front feet. When a bear suddenly charges from a stationary position it uses a half bound. Its hind feet propel the bear as in a leap, and the front feet support it on subsequent landings, after which they add propulsion with their own leap. Because of a bear's large size, there is only one brief aerial phase after the hind leap. When the front leap occurs, the hind feet are already back on the ground, and there is no second unsupported phase. There also is considerable lead between front couplets in a half-bounding bear, and its back remains fairly stiff throughout this gait, unlike the weasel's full bound. Whereas bears charge (rapid acceleration) using a half bound, they run for longer distances at steady-state speeds using a conventional gallop. Based on mechanical modeling and theoretical calculations, Alexander *et al.* (1980) suggested that the bound is an energetically expensive gait compared to galloping, but these authors admit that their models do not account for the ability of the muscles of the back and trunk to assist in locomotion.

Except for charging bears and running proboscidians, the *gallop* is essentially the universal high speed running gait of large mammalian quadrupeds. In the gallop there is considerable lead in both the front and the hind feet, and there are one or two unsupported phases. Two types of gallops are recognized: *transverse* and *rotary*. In the transverse gallop the leading foot in each couplet is on the same side of the body. It seems to be more stable than the rotary gallop and tends to be used by larger mammals in general, and by smaller mammals while running at slow speeds. In the rotary gallop, lead feet are on opposite sides of the body, and in a footfall diagram it can be seen that there is a rotary pattern in the timing of each foot striking the ground (i.e., left rear, left front, right front, right rear, then repeated)(see Hildebrand 1977). The rotary gallop is theoretically less stable but appears to offers greater maneuverability. Probably for these reasons, it is favored at higher speeds, where increased momentum helps maintain stability, and by smaller mammals, which are inherently more stable. Large predators use the rotary gallop to chase prey, probably because it facilitates greater maneuverability (Hildebrand 1985a).

The *canter* is a special kind of slow gallop during which there is considerable distance between leading and trailing feet in each couplet (cantering animals often appear to have either a hesitation or a

head bobbing motion in their stride). However, in a canter one diagonal set of fore and hind feet touches the ground at nearly the same time, like in a trot, while the other diagonal pair swings out of phase with each other. The canter can be used at surprisingly slow speeds, and is employed mostly by ungulates that engage in sustained moderate speed travel during migrations, including blue wildebeest and plains bison (*Bison bison*) (Pennycuick 1975, Guthrie 1990a). For migrating ungulates, the canter is the functional equivalent of trotting in a carnivore. Because the canter is essentially a gallop, it can be used to modulate smoothly between fast and slow speeds without changing gait, facilitating quicker and smoother acceleration/deceleration. The only carnivore I know that regularly uses a canter is the spotted hyena (Kruuk 1972, Mills 1989), and in the next chapter I discuss how this relates to its back and limb proportions and the weight of its head and neck. There I will show that the pace and canter go hand-in-hand for spotted hyenas, as they may have for short-faced bears.

Duty factor, the fraction of the stride cycle that each foot is on the ground, is an important concept in running gaits because it reflects the amount of time each foot has to dissipate vertical ground forces imparted on the limbs (and thus the instantaneous velocity of these forces). Later, I will show that these forces are disproportionately greater in larger animals and at higher speeds and that the gaits of large animals traveling at high speeds are dictated in part by the need to manage these increased forces. For instance, this is probably the reason why large mammals, over about 250 kg, have only one unsupported phase per stride in their gallop (occurring when the feet are gathered beneath the body— during extension, one or more of their front feet hit the ground before the last hind foot leaves the ground). Smaller mammals tend to have two aerial phases per stride— both when the legs are gathered beneath the body and when they are extended. The number of aerial phases also seems to be correlated to back flexion. When galloping, nearly all carnivores (except bears— see below) have both gathered and extended aerial phases because the spine flexes and extends with the legs. Most ungulates do not flex the spine much and are not aerial during the extended phase (Hildebrand 1960, 1977).

Hildebrand (1977) concluded that bears use a transverse gallop. However, I have studied films of running brown bears of various sizes, and slowed the film speed down to observe footfall patterns. All the bears in these films used only a rotary gallop (unpublished data), just as other large carnivores do (Hildebrand 1977). However, there typically is less lead the hind feet couplet of a galloping bear, compared to other carnivores. Also, bears only have only one aerial phase (the gathered phase) when galloping, probably because their large size prohibits them from flexing their backs and achieving a second aerial phase during extension. Smaller carnivores, such as felids and canids, use both aerial phases (gathered and extended)(Hildebrand 1960, 1977). The lack of a second aerial phase in polar bears and brown bears suggests that large extant bears experience limitations to galloping abilities. I will argue in later sections of this chapter that this is because they approach structural limitations of their bones in

relation to the very large dynamic stresses of locomotion incurred by bears due to their large size. A charging bear, as noted, usually will accelerate using a half bound— essentially a series of leaps off the hind limbs whereby the weight is supported during landing by two largely out of phase front limbs. The difference between a half-bound and gallop, however, is not great in an animal like a brown bear where there is little back flexion. Essentially, the only difference is that there is noticeable lead in the hind limbs during a gallop but not during a half-bound.

5. Preliminary Remarks on Scaling and Allometry

The effect of body size on function, or scaling, is a particularly critical factor impacting an animal's locomotor abilities. Practically every aspect of locomotion is directly affected by body size, and large size, especially, is a double-edged sword: it affords an animal certain energetic and spatial benefits, but very large animals also face a host of structural thresholds which limit high force locomotor activities. Scaling effects and references to body size allometries will arise throughout the remainder of this and the next chapter, so a review of allometry and remarks on scaling principles seem in order.

Allometric Functions

Consider two related parameters (x and y) of an animal's shape, physiology, or performance, such as a long bone's length and width. One can describe the relationship by which their values co-vary over a range of sizes by the allometric (power) equation:

$$y = b \cdot x^{\alpha} \qquad (1)$$

This equation yields a curvilinear relationship between x and y where α is the power function, or allometric constant, and b is the y-intercept. Untransformed data also can be fitted to a linear equation

$$y = ax + b \qquad (2)$$

but this line often has a poorer statistical fit to the data because body shape does not change in a linear fashion over a large size range. Thus, the slope (a) does not remain constant (i.e., the slope of Equation 2 is an average slope). Using Equation 2 to describe untransformed data is equivalent to forcing a rectilinear fit to curvilinear data.

Typically in allometric studies one is testing the hypothesis that the data fit a particular equation.

or line, such that the values of y and x are driven by a conserved allometry over a range of sizes. That is, the following proportion remains constant:

$$\frac{(y_2 / y_1)}{(x_2 / x_1)} \tag{3}$$

In scaling discussions biologists often are not concerned with the precise values of x, y, or the y-intercept (but see Gould 1971 for why these can be important). Instead biologists apply the most biological meaning to the slope (of log-transformed data) because it indicates the proportionality of x and y, as per Equation 3. Statistically, and visually, this sometimes is easier to do if Equation 1 (a power function) is logarithmically transformed into the linear equation:

$$\log y = \alpha \log x + \log b \tag{4}$$

where α is the slope of the line and b is its y intercept. Log-transforming the data also can help to normalize their variance (Lasiewski and Dawson 1969). This allows one to perform parametric statistical tests on the data, commonly a least squares regression, to test their fit to a specified line or slope (the hypothesis). Some authors have rightly questioned whether the data should always be log-transformed (see discussions in Lasiewski and Dawson 1969, Smith 1980, Harvey 1982, and Calder 1984). I think this is an important issue, and will be discussing it more at the end of this section. As a general procedure, *both* linear and power functions should be derived for the untransformed data; if the correlation coefficient (r^2) and p-value are substantially better for the power function, then the data should be log-transformed for linear statistical analyses. (Alternatively, non-linear statistical tests can be applied directly to the power function.)

Similarity Hypotheses and Scaling Theory

Biologists from diverse fields have invested considerable effort into the theory of allometry, proportionality, dimensional analyses, and similarity hypotheses— that is, the regular manner in which animal shape and function change with body size (see summaries in Thompson 1942; Huxley 1932; Gould 1966, 1971; Gunther 1975 Economos 1982, 1983; Calder 1984; Schmidt-Nielsen 1984; and papers listed below by McMahon and Alexander). Similarity hypotheses, in general, predict that animal proportions will change with size in systematic, or "similar" ways.

Early in their training, biologists are indoctrinated into the concept of geometric similarity and its predictions about animal shapes at different sizes. This concept states that according to geometric principles, as an animal is scaled up or down, its structural surface areas (s) should vary with linear

dimensions (l) as $s \propto l^2$, and its structural volumes (and masses) (m) should vary as $m \propto l^3$. Accordingly, structural surface areas should scale to masses (of the whole body or specific structures) as $s \propto m^{2/3}$ — the famous two-thirds rule.[3] It follows that geometrically similar animals will have different sizes but similar shapes, and thus are termed isometric (*iso* = same, *metric* = measure). The slope (α) of a plot comparing two linear dimensions in isometric animals will be 1, because changes in the proportions of y are equal to changes in the proportion of x (Equation 3). The slope of a line relating a surface area dimension to a linear dimension in two such animals will be 2, and a line relating a volume (mass) dimension to a linear dimension will have a slope of 3 (on a logarithmic scale).

The two-thirds rule of geometric similarity predicts that as animals are scaled up in size, functions which are dependent on surface areas (e.g., gas and fluid absorption rates, bone strength) will not keep pace with increases in functions that scale proportional to volume or mass (e.g., cellular respiration rates or the forces exerted by the body's weight). For these very reasons, one might predict that animals generally should not be built geometrically similar (isometric) over a large size range— rather, they should be built allometrically (*allos* = different). Allometric scaling implies that related animals of different size also will have different shapes, or proportions. Changes in shape (deviations from geometric proportions) may be interpreted as ways that morphologically similar animals try to maintain adequate levels of performance at dissimilar sizes to compensate for the two-thirds rule. This has led biologists to wonder if animals perhaps scale according to some other principle of similarity— in other words, is animal shape responding to changes in body size in a systematic way other than geometric similarity?

The theory of *static stress similarity* (originally proposed by Galileo) predicts that surface areas should increase as l^3 to keep pace with increases in mass, but this theory has been shown to be a poor predictor of animal shape (Gunther 1975, McMahon 1975a, Schmidt-Nielsen 1984). Today, the leading alternatives to geometric similarity are the theories of *elastic similarity* (Rashevsky 1962, McMahon 1973, 1975a) and *dynamic similarity* (Gunther 1975, Alexander and Jayes 1983, Economos 1983). The most rigorous tests of these competing similarity hypotheses have been conducted on limb bone dimensions in mammals, but their implications have been extended to most other aspects of scaling and allometry (Gunther 1975).

Elastic similarity borrows from engineering principles which state that solid support structures should be proportioned with the ability to dissipate static bending stresses and resist bucking (Rashevsky 1962). Biological elastic similarity theory predicts that animal structures should be scaled to experience similar degrees of elastic deformation during support and locomotion. In plants, the lengths and diameters

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[3] Traditionally, theoretical scaling exponents are expressed as fractions and empirically-derived exponents are expressed as decimal values. This convention will be followed throughout the text.

of trunks and limbs seem to scale well according to properties of elastic similarity (McMahon 1973), and McMahon extends the logic to animal design (McMahon 1975a, 1975b). An important prediction of elastic similarity is that lengths and diameters (such as in a bone) should scale as $l \propto d^{2/3}$ (geometric similarity predicts $l \propto d$), meaning limbs will get proportionately wider as animals are scaled up. Since m must be proportional to $l \cdot d^2$, elastic similarity predicts that $l \propto m^{1/4}$.[4]

Alexander's and his colleagues have demonstrated a number of inadequacies of the elastic similarity model and they question the premise that animal structures will respond to elastic strain forces in ways similar to plants and I-beams. They also contend that elastic similarity primarily addresses static stresses, and does not adequately account for dynamic forces incurred during locomotion (Alexander 1977, 1985; Maloiy *et al.* 1979). However, McMahon (1975b, 1977) has developed a spring model that extends elastic principles to dynamic systems. Alexander argues that animals should be scaled so that homologous parts on different sized animals experience equivalent net forces (strains) during locomotion and support — that is, they should scale to be "*dynamically similar*." Alexander and Jayes (1983) specifically state that under the laws of dynamic similarity the motions of two different sized animals could be made identical by multiplying all linear dimensions by one constant, all time intervals by another constant, and all forces by a third constant. Later I will show how animals which run in dynamically similar ways do so by modifying their range of motion more than their morphology.

Reservations about Scaling Applications

It is not my intention to review or refute the various scaling hypotheses. I bring them up to raise the point that biologists still are uncertain about the precise nature of how size affects shape and function, and because I am skeptical about the *a priori* assumption that animals will follow scaling laws, especially above the species level. Indeed, allometric constants have been measured for numerous morphometric features across a great diversity of animals, yet the data do not unequivocally support one similarity hypothesis over the others. For instance, Alexander (1977), Alexander *et al.* (1979), and Biewener (1982, 1983a) have shown that limb bone length and diameter generally scale geometrically. However, the limb bones of artiodactyls, especially bovids, are an exception and scale better according to predictions of elastic similarity, and some specific bones, especially metapodials and femurs, can be completely aberrant (McMahon 1975b, Alexander 1977a, Alexander *et al.* 1979, Garland 1983). Kinematic parameters related to gait, such as stride frequency and limb excursion angles, also tend to scale according to elastic similarity (Biewener 1983a). However, maximum running speeds in mammals scale to body mass in

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[4] If $l \propto d^{2/3}$, then $d \propto l^{3/2}$. Substituting l for d in the equation $m \propto l \cdot d^2$ yields $m \propto l \cdot (l^{3/2})^2$ which is equivalent to $m \propto l^4$. l then becomes proportional to m as $l \propto m^{1/4}$.

closest agreement with dynamic similarity (Garland 1983), suggesting that animals do, in fact, run in ways such that homologous parts experience equivalent forces and strains. This will be an important consideration when comparing *Arctodus* to other smaller carnivores because as animals get larger, dynamic forces increase faster than the strength of support structures (bones). I will show that *Arctodus* did not evolve the bone strength necessary to handle the dynamic stresses of high force activities such as acceleration, maneuvering, or running at very high top speeds, all of which are implied directly or indirectly by predatory models for *Arctodus*. This is an important point that I will return to frequently.

Throughout this and the next chapter, I will need to refer to theoretical and empirical scaling relationships and the consequences of large size. However, I have a number of reservations about the use of scaling functions and allometry. First, there is a tendency to seek linear equations or simple exponential functions to describe relationships that are complex and which may better fit a polynomial equation (if any equation at all). This has been the case, for example, for the relationship between body size and maximum running speed in mammals (Garland 1983). To some extent, there is a tendency for larger mammals to have higher top speeds, but after attempts by previous authors (e.g., Bakker 1975) to derive a linear allometric relationship between maximum speed and body size, Garland showed what should have been obvious— that maximum running speed is not a simple (single order) linear function of size. Otherwise, the largest animals would also be the fastest. Garland's data show that maximum speed fits a second order polynomial (quadratic) equation and tends to increase with size up to about 119 kg, after which it declines. I will be examining this pattern in detail in subsequent sections because it suggests that there is an upper limit to body size in predators (Garland's data is discussed in more detail later in this chapter).

Furthermore, using logarithmically transformed data, while necessary for some statistical analyses, can be misleading. This is because the magnitude of residuals is not as apparent in plots of log-transformed data. In such plots, large and biologically significant deviations from a regression line become masked, especially when data are plotted over a large range of body sizes (the effect is seen most in the small-bodied animals in these plots). In fact, that is why a log-log regression often looks like such a good fit to a data set.

Moreover, allometric constants derived for multiple taxa represent *average* slopes, and indicate the way that body proportions or functions *generally* change with body size. They reflect, but they do not indicate, actual values, and averaging values over a wide range of taxa washes individual species allometries. Stated another way, an averaged interspecific allometry may not resemble any of the actual individual allometries it supposedly represents (interspecific allometries are epiphenomena— see Fig. 6f and further discussion below). Still, biologists frequently seek universal principles in interspecific allometric slopes rather than looking for ways that species deviate from these slopes. Yet, this often is where the real biological information lies. For example, allometry has been used to investigate the manner

in which muscle mass scales to body mass. In mammals, muscle mass $\propto m^{1.0}$ (Calder 1984). Emphasis is placed on the meaning of the exponent, 1, and the idea that perhaps a single relationship between muscle mass and body mass can be found among mammals. Yet, this general allometric equation for muscle mass in mammals predicts muscle mass in any given species very poorly. Lions, for instance, have the greatest percentage of muscle mass measured in any mammal— about 62 % (Davis 1962). These types of patterns either are not apparent from allometric data or they are not emphasized as much as the scaling exponent, yet they are very important biologically.

Arguing along these lines, Davis himself (1962:511) remarked, "To me it seems unrealistic to assume a universal growth constant (α) for organs, such as the heart, whose size is directly related to performance. It is possible, of course, to determine a mean value ... but it does not follow that the mean value has any biological significance." Even Alexander (1985:37) commented, "It seems unprofitable in any case to persist in looking for similarity principles. There is no reason to expect evolution to seek similarity as such. Rather it seeks some kind of optimality."

Because of the above reservations, I will be using scaling principles conservatively, and I prefer a loose meaning of the term scaling, whereby I refer to the fact that there are natural dimensional consequences of changes in body size— namely that linear dimensions, surface areas, and volumes (masses) will increase at differing rates, with real functional consequences. As alluded to above, it is the predictive and axiomatic side of scaling that I am dubious about— the notion that animals across broad taxa will respond to body size changes in systematic and predictable ways, and that their evolution is somehow bounded by scaling laws. With arguments about non-Darwinian evolution aside, it seems most reasonable to assume that an animal's individual shape and proportions evolve not as functions of similarity laws, but as function of selective forces acting on the realities of its size, in conjunction with its phylogeny and niche.

There is little reason to suspect that scaling rules and similarity laws will supercede selection or that an animal is tied to its allometry. Rather, allometry (or more accurately, proportionality) is like any other character that changes in response to selective pressures, and I believe that the most appropriate use of allometry and scaling are in the *a-posteriori* study of these changes. One may think of it this way: *scaling principles predict some physical ramifications of body size changes, while the study of allometry reveals how animals have or have not dealt with those realities through their evolution*. For instance, Kurtén has used allometry in many studies (including Kurtén 1954, 1955, 1967b, 1970; Kurtén and Rausch 1959) to show that lineages may retain similar allometries as body size evolves over short periods of time, but that after long periods of time or in response to large changes in size, allometries change as species diverge. Kurtén held no preconceived notions about scaling laws, but instead looked at the direct functional reasons for why animals have evolved certain proportions in consideration of body size

(however, he also used allometry to test phylogenetic hypotheses in the fossil record).

Functional Interpretations Using Allometry

With the preceding caveats in mind, I next want to offer some functional interpretations that can be made by comparing allometries between species or subspecies. The ideas in this discussion will not be applied until the next chapter, where *Arctodus*' limb proportions are compared to other bears using allometric techniques. But since the discussion is theoretical and provides a general review, it is included in Part I.

In any allometric comparison among taxa, one must be clear in distinguishing between two confounding forces acting on the allometry— phylogeny and function. Both phylogenetic and functional hypotheses can be tested using allometry, but when functional hypotheses are being tested one needs to be clear about the taxa's phylogenetic relationships so their influence can be gauged. However, if the phylogenetic relationships among the taxa in question are unclear, interpretations of function may be dubious. For instance, if two taxa are closely related or of direct ancestry, it is likely that one allometry descended from the other, and any differences in proportions for the structure in question may signify either a functional change or compensatory growth (growth in larger individuals that yields different proportions— usually structures that are more robust— in order to retain similar function as smaller individuals). Alternatively, the allometry and/or proportions of the descendent taxa simply may be an extension of the ancestral allometry without change, in which case it is probable that not enough time has elapsed since speciation for selection to significantly impact body proportions— only body size has changed. If two more distantly related taxa are being compared, then one allometry is not assumed to be descended directly from the other and it can be concluded that any differences are functional and that any similarities in proportions may represent functional convergences.

My concern is these chapters is principally about function, not phylogeny. Therefore, I will be comparing not just the nature of allometric lines, but also their implications to actual structural shape and performance (i.e., real proportions). Along these lines, it is important to reiterate that a straight line of allometry on a logarithmic scale does not imply that a structure's shape is held constant over a range of sizes (unless $\alpha = 1$), but rather that its shape is changing with size in a regular fashion, and that this has functional implications. In the case of a long bone, if $\alpha > 1$ then the bone grows relatively wider as size increases, if $\alpha < 1$ it grows relatively narrower. Recall from Equation 3 that the slope of log-transformed data also can be conceptualized in terms of the non-transformed data as the conserved ratio of the proportionality of one variable (y) versus the proportionality of the other (x) (Smith 1980) (also note for subsequent discussions that by definition α is both the slope of the log-transformed data and the exponent of the power function derived from untransformed data).

Smith (1980) and Harvey (1982) both have shown that linearity is not always improved by log-transforming data nor does this necessarily produce a better fit to the data. Furthermore, relationships which are linear before log-transformation will remain linear when plotted on a log-log scale. In Chapter 3, I will present allometric data for various bears and depict them on a linear (non-log) scale because their trends are nearly linear without transformation. Correlation coefficients for bone length vs. width in those data are essentially identical when either linear or power functions are derived. So, while non-transformed data in presented, I will discuss them in terms of α because α is a constant function of proportionality which is independent of scale or units. This is a requisite to test certain biomechanical and evolutionary hypotheses based on proportionality when comparisons are being made between animals of varying size and between different bones. The slopes of untransformed data could not be used for these comparison in most cases because they represent absolute, not relative, proportions and thus are not comparable over wide ranges in size.

Five modes of allometric comparisons are shown in Fig. 6 for the hypothetical relationship between length and width of a structure such as a long bone in two species or subspecies (*a* and *b*). Figure 6a depicts a simple example of two species that differ in body size but have identical α and *y*-intercepts. This pattern is commonly seen in closely related species of recent descent where the change in body size is not great or where the divergence occurred very recently (Kurtén 1967b). As long as $\alpha \neq 1$ then the shape of the bone in species *b* will be different than in species *a*. Functionally, this means that species *b* has made no change to the allometry of this structure in order to compensate for its larger size. Over time, one would expect that natural selection would lead to a compensatory change in allometry which would give species *b* similar performance but different shape, as long as the structure's function remained the same. Since this has not occurred in the species depicted in 6a, one may conclude that selection has been for a new function or performance level in the structure (especially when the difference in body size is large or when the two species are distantly related), or more likely that the two species only recently diverged. When the latter can be ruled out by other evidence, then a change in function or performance can be inferred.

Figure 6b depicts two *equal-sized* species which have the same α but different *y*-intercepts. The structure in an individual of species *b* will be absolutely wider than in a similar-sized individual of species *a*. From a performance standpoint, if the structure is a long bone then it will be stronger but also relatively heavier in *b* than in *a*. The allometries of *a* and *b* are different in this case, but the difference does not compensate for a change in body size, since both species are the same size. In other words, the allometry of species *b* cannot be explained as a means of retaining similar function and performance as species *a*. Instead, one would conclude that selection has favored a more robust limb in *a* vs. *b* for functional reasons.

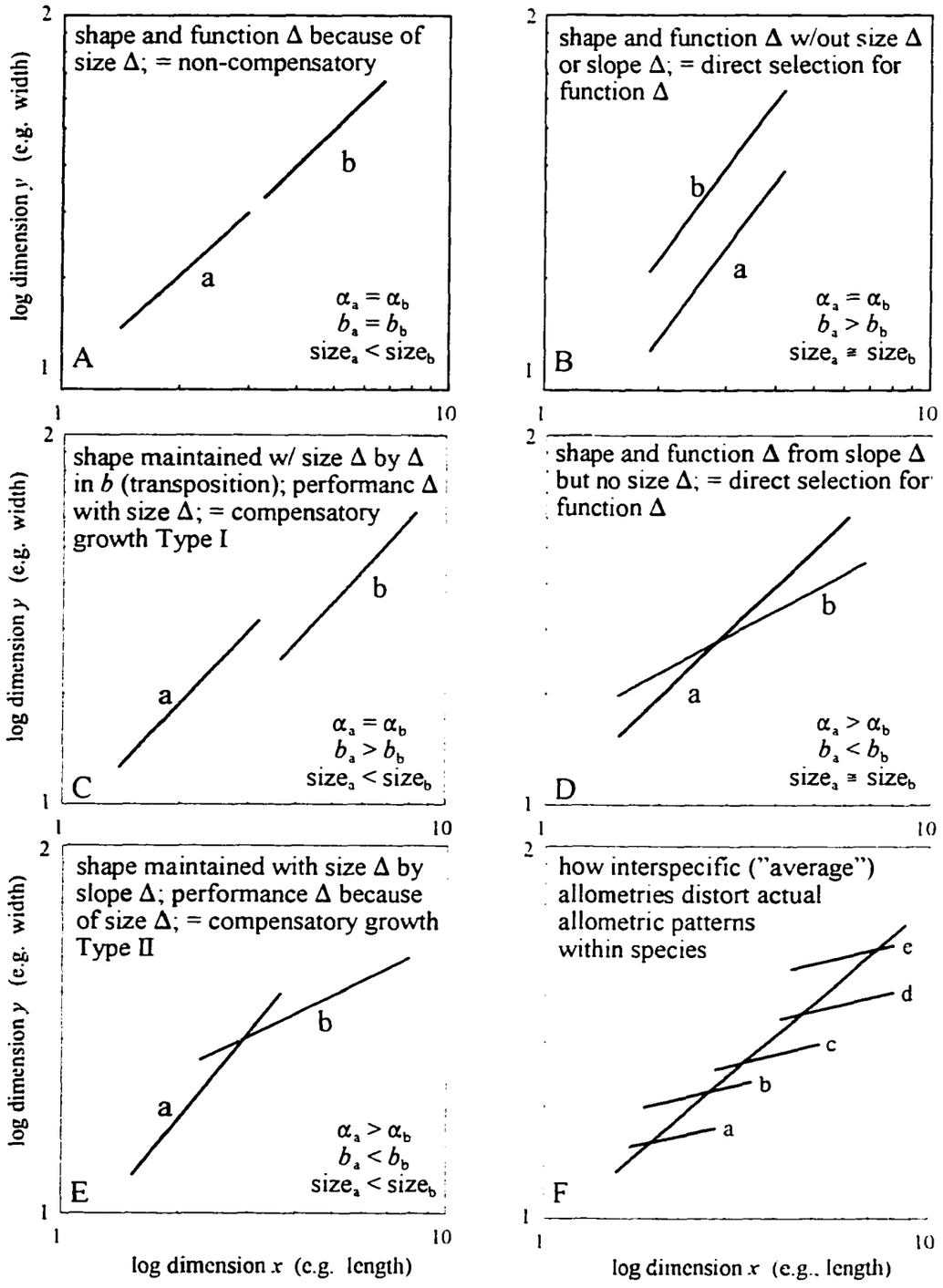


FIGURE 6. Five modes of allometric comparisons for two species or subspecies (*A* - *E*). *F* shows how interspecific, or average, lines of allometry usually yield slopes and *y*-intercepts that do not reflect the actual values for any given species because interspecific lines simply connect the average allometries for each of the individual species. See text for discussion. (*F* modified from Gould (1971)).

A common form of compensatory growth is shown in Fig 6c. Here two species of *different size* have similar α, but different y-intercepts. This strategy has been interpreted as a means by which large animals retain proportions similar to smaller relatives (Kurtén 1954, Gould 1971). Consider the allometry of species *a*. Its α is > 1, which is typical for long bones, meaning that the structure being measured gets relatively wider (more robust) in larger individuals of species *a*. If species *a*'s line of allometry were extended to the size range of species *b*, the structure's proportions would become increasingly divergent from the norm. Presuming that the shape of the structure is adaptive, this simple extension of line *a* would change the performance of the structure, as I discussed for the example in 6a. In order for a larger version of species *b* to retain a similar (geometric) shape, its allometry needs to be "transposed," as this type of compensation has been termed by Meunier (1959a, 1959b in Gould 1971). Kurtén (1954) also noted this pattern of allometry and its compensatory effect on the dentition of two closely related bears, cave bears and brown bears. However, in subsequent sections of this chapter I will be reiterating an important point: that *similarity in performance does not arise from similarity in shape, especially over very large ranges of body size*. This is why α values of 1 are uncommon for linear dimensions and why lines of allometry can only be conserved over a narrow range of body sizes— the larger α is, the narrower the size range. Furthermore, even compensatory growth, which maintains similar proportions between species, will lead to a change in functional performance because, as I will show, a geometrically scaled structure does not perform the same in a large and small animal.

Figure 6d presents a case of two *similar-sized* species with *different* α. Because there is no size disparity, the differences in allometry can not be interpreted as compensatory but must reflect a difference in performance or function for the structure. A change in α which may be interpreted as compensatory (for size differences) is depicted in 6e. In this case, the structure in species *a* may become too wide for practical use if extended to the size range of species *b*. As many authors have pointed out (e.g., Kurtén 1967b; Gould 1966, 1971, Schmidt-Nielsen 1984; Calder 1984), this leads to monstrosities. In these cases, compensation is perhaps more a matter of accommodation, rather than a strategy to achieve similar performance. If both species are fast running coursers, for instance, and α of species *a* > 1, then the bone is getting relatively heavier with increasing size. Perhaps when reaching the size of species *b*, the additional weight becomes considerable, and a change in allometry has evolved to keep the limbs light. This may help species *b* to remain swift, but in later sections I will discuss how this implies compromises to other features of the limb, including its strength. So while species *b* compensates to retain certain kinematic advantages, it will need to curtail other activities relative to species *a*, such as making sharp turns, accelerating rapidly, or even running at slower speeds (see Sections 7 - 10).

All of the above conclusions apply strictly to allometries constructed for individual species or subspecies, not allometries constructed for multiple species. Such an interspecific line of allometry, or

"average" allometry, does not accurately quantify the way that shape will change with size in any of the species or individuals involved. Rather, interspecific allometries are epiphenomena, even when closely related taxa are involved, such as within a single genus. This is because allometries are inherited, meaning they are shared only at the level of species and below (Gould 1971). Figure 6f demonstrates why this is so. There it can be seen how interspecific slopes essentially connect the median points of individual species allometries. So within each species or subspecies, one may determine the genetically determined ratio of proportionality (allometry), but, as Fig. 6f shows, even if a straight line of regression can be drawn through multiple species, this line does not accurately match the ratio of proportionality in any of the individual species. As discussed above, this is because animals evolve differences in allometry (i.e., transpositions, changes in α) which reflect the way that functional needs change with size.

The discussions in this section were intended to provide a sense for the way that scaling principles and allometry are used to investigate the functional effects of changes in body size and body proportions. What follows is a review of some specific body size-dependent factors of locomotion, including the effects of scaling on energetics, the ability of muscles to generate force, and the structural limitations of bones.

6. Energetics, Metabolism, and the Cost of Locomotion

There are various ways to look at energy expenditures during locomotion and account for the costs of transport. On one level, biologists speak of the amount of energy consumed (total, rate, or instantaneous) during locomotion, which physiologists often measure as the amount of oxygen consumed by an animal. At another level, biologists speak of the mechanics of locomotion, that is, the exchange of metabolic energy for mechanical work as performed by an animal's muscles. The ratio of these two—metabolic energy input versus work output— equals muscular efficiency. In this section I will be discussing whole body energetics, both in terms of metabolic inputs and work outputs, and I will review the mechanics of this energy conversion. I will show that the efficiency by which animals convert energy to work varies regularly with size. In the subsequent two sections I look specifically at the way muscles generate force for locomotion and how the skeletal system deals with these forces, especially as animals get larger.

Setting the Stage

Hill (1950) set down a series of classic hypotheses regarding locomotor costs and body size based on dimensional analyses (scaling). Many of Hill's ideas still form the premises being tested in modern

experiments on animal locomotion, so they are worth repeating. Starting with the assumption that the properties of individual muscle fibers do not vary among species or animals of different size, Hill used geometric scaling principles to predict that all animals, regardless of size, should be capable of achieving the same absolute levels of performance for certain locomotor skills. Specifically, Hill predicted that all animals should theoretically be able to achieve the same absolute top speeds and jump to the same absolute heights, but the muscles of small animals should consume energy faster and perform work at higher rates than large animals. This latter prediction indicates that smaller animals should fatigue more quickly and after covering shorter distances. Taylor *et al.* (1982 pp. 2) summarized Hill's logic as follows: "each gram of muscle performs the same amount of work and uses the same amount of energy during a step, but the small animals have to take many more steps to cover the same distance because of their shorter legs. Therefore, when running at the same speed small animals should have higher stride frequencies and consume energy at higher rates." I will discuss how modern analyses have shown Hill to be wrong on a few of these points and correct on others, but often for the wrong reasons.

The Cost of Transport

Locomotor physiologists have established that the mass-specific rate of energy consumption increases with speed but that the rate of increase is inversely proportional to body size (Fig. 7)(Schmidt-Nielsen 1972; Taylor *et al.* 1970, 1982; Taylor 1977; Kram and Taylor 1990). Data from these studies also show that the "incremental cost of transport"— the amount of energy consumed while moving a unit of body mass a given distance— decreases as body size increases. The incremental cost of transport scales $\propto m^{-0.40}$ according to Taylor *et al.* (1970), $\propto m^{-0.316}$ according to Taylor et al (1982), and $\propto m^{-0.25}$ according to Kram and Taylor (1990) (Fig. 7a). The incremental cost of transport must be distinguished from the "cost coefficient" of locomotion, which is a constant and equals the rate of energy consumption by each kilogram of body mass during steady state locomotion, independent of distance traveled. This value is mass independent ($\propto m^{0}$) so it is the same for animals of all size (Fig. 7c) (Taylor *et al.* 1982, Kram and Taylor 1990). Therefore, while animals expend about the same amount of energy per kilogram per step at physiologically equivalent speeds, small animals take more steps to cover a given distance. Physiologically equivalent speeds are speeds at which equivalent locomotor events occur in different animals, such as changing from a trot to a gallop or running at top speed— these do not occur at the same absolute speeds for all animals, but the events are considered to be a physiologically equivalent (Heglund *et al.* 1974). Often it is most meaningful to compare the energetics and stride traits of different sized animals at physiologically equivalent speeds, rather than absolute speed.

Kleiber's (1961) well-known comparison of basal metabolic rate (M_b) and body size also shows a negative scaling relationship (mass specific $M_b \propto m^{-0.25}$; whole body $M_b \propto m^{0.75}$), so it is not surprising

that a similar relationship holds for locomotor metabolism. This relationship should not be taken to mean that large animals are metabolically more efficient than small animals. First of all, as Calder (1984) pointed out, efficiency is a dimensionless term that implies a ratio of input versus output; comparing just mass-specific energy inputs (which is what metabolic measurements do) says nothing about outputs. But probably more important, comparing energy consumption between large and small animals potentially leads to the pitfall of doing so without regard for the way that physiological time, space, and rates scale to body size (Calder 1984, Lindstedt and Swain 1988). For instance, while larger animals consume less energy *per kilogram* per kilometer during a given activity, they invariably perform that activity for a longer time, over a greater distance, and over a longer lifetime— and they have more kilograms to move. It turns out that over the course of their lives, large and small animals spend about the same amount of energy to support a unit of body mass, regardless of size (Calder 1984). This does not mean that large animals do not incur certain benefits for their size. Indeed, they are able to take advantage of a larger home range and its greater spatial diversity, and large animals can more readily make large scale migrations (Lindstedt and Swain 1988). Reciprocal arguments can be made for the advantages/disadvantages of being small. It is important to emphasize that these statements only hold true for metabolic input, not work output. Later I will discuss how large and small animals differ considerably in their inherent abilities to engage in certain locomotor activities simply due to their size, and that large animals are more efficient locomotors because they are better able to utilize elastic strain energy.

Mechanics of Walking and Running

Next, I turn to the mechanisms by which metabolic energy is converted into work during locomotion. As an animal walks or runs, energy is expended to accelerate and decelerate different parts of the body relative to each other and relative to the ground. In this regard, energy is used primarily for two tasks: 1) lifting and accelerating the body's mass against the vertical forces of gravity (since the body's mass rises and falls with each stride), and 2) accelerating/decelerating the limbs relative to the body's center of mass (Manter 1938; Cavagna *et al.* 1964, 1977a, 1977b; Alexander 1977b; Heglund *et al.* 1982a). The energy expended to lift the body's mass seems to account for most of the energy expended during locomotion, although there is some disagreement in the literature regarding the relative importance of these two expenditures (Taylor *et al.* 1980). For instance, Manter (1938) trained cats to run over force plates and found that the energetic component of moving the limbs varied from almost 0 to > 25 % of total energy expended, the most important factor being the animal's speed and rate of acceleration. Using similar apparatus but more species, Cavagna's group and others have concluded that the cost of lifting the body's mass can be over 10 times the cost of swinging the limbs (Cavagna 1977a, Taylor et al 1980, Farley and Taylor 1991). In a four-part study, Heglund, Taylor, Cavagna, Fedak, and

Maloiy attempted to account for the costs of locomotion in 15 homeotherms by simultaneously measuring the metabolic energy consumed during locomotion, the work performed to lift the body's mass, and the work performed to swing the limbs (Taylor *et al.* 1982; Fedak *et al.* 1982; Heglund *et al.* 1982a, 1982b). They found that swinging the limbs may account for as little as 3 % or as much as 30 % of the applied forces, and like Manter's data, the most important determinant was speed (they did not test acceleration). Alexander *et al.*'s (1980) theoretical calculations also show that the cost of moving the limbs can be fairly high. Anatomists (e.g., Smith and Savage 1956, Hildebrand 1985a, 1985b, 1995) tend to emphasize the cost of accelerating/decelerating the limbs, not necessarily to discount other costs, but more to show the relative costs of limb oscillation between animals of different builds. I will return to these points in the section on kinematics, where it will be shown why the cost of swinging the limbs increases with speed.

Walking: When an animal uses a walking gait, its center of mass rises and falls, during which kinetic energy (E_k) is exchanged for gravitational potential energy (E_p). As the animal lifts its mass, E_p increases and E_k decreases, by which they are said to be out of phase. When the body mass falls again, E_p decreases and E_k increases. The process of walking depends on capturing this E_k as forward momentum by leaning the body's mass forward. Up to 70% of the E_p may be recovered in this way (Manter 1938; Cavagna *et al.* 1964, 1977a; Heglund *et al.* 1982a). These mechanics are analogous to the exchange of E_k and E_p in a pendulum or rolling an egg end over end; when an animal walks it only performs work to "keep the egg rolling" (analogy of Cavagna *et al.* 1977a, pp. 260). Later I will show that there is an optimal walking speed for this energy exchange and it increases with leg length, which partially explains why long-legged animals naturally walk at higher speeds but with slower stride rates.

Trotting and Pacing: Running is energetically and mechanically quite different than walking. When an animal runs using a *trot* or a *pace* there is almost no transfer between E_k and E_p because both rise and fall in phase. That is, when the body mass is lifted, E_p rises but so does E_k. This occurs because E_k is converted to elastic strain energy in tendons of the leg during each footfall and is recovered again at the end of each footfall when the body mass is lifted. Both E_p and E_k are highest at the body mass's highest point, and both fall as the body falls (E_k falls because all of the elastic strain energy has been consumed). Because of this stored elastic energy, the running trot/pace is analogous to a spring or a bouncing ball, not a pendulum (Cavagna *et al.* 1977a, 1977b).

Galloping: The running trot/pace relies heavily on a spring-like mechanism and recovery of elastic strain energy, but when a running animal changes from a trot or pace to a gallop it utilizes both pendulum and spring mechanisms. The shift in energy phases at the trot-gallop transition is a result of the acceleration process when an animal changes from a steady state trot/pace to higher galloping speeds. The exchange between E_p and E_k during this transition is used to elevate the animal's body mass even higher and to increase forward velocity— therefore, there is a bounce and a lift. As the animal increases speed,

E_k and E_p become more in phase (they rise and fall together) and purely spring dynamics take over again, whereby elastic strain energy is used to perform much of the work. But whereas the steady state trot/pace is analogous to a single spring, the steady state gallop works like two springs because the two front and two hind limbs function as independent pairs with two bounces (energetic cycles) per stride.

Locomotor Efficiency and the Role of Stored Elastic Strain Energy— Advantages of Being Big

I now have examined some of the metabolic requirements of locomotion in regards to mass and speed, as well as the general way that energy is used by animals to propel their mass. Next, I want to look at the efficiency by which muscles convert energy into work. Throughout this and subsequent sections I will rely on the well established fact that individual mammalian muscle fibers have essentially identical performance properties in all species (Hill 1950; Alexander 1973, 1977b; Cavagna *et al.* 1964, 1977b; Heglund and Cavagna 1985).

Typical striated muscle fibers are capable of converting metabolic energy into usable work at about 25 % efficiency; the balance is lost as heat (Heglund and Cavagna 1985). But when energy consumption and amount of work performed are measured in running animals, muscular efficiency appears to increase as body size and speed increase, and exceeds 25 % (Fig. 7) (Taylor *et al.* 1982, Heglund *et al.* 1982b). These authors show that the mass-specific energy consumption *per kilometer* decreases with size for animals running at equivalent speeds, whereas the mass specific rate of work performed *per kilometer* is independent of body size (Fig. 7 a and *b*). Looking at these relationships on a *per step* basis, rather than per kilometer, it is apparent that mass-specific energy consumption is independent of body size and mass-specific work performed increases with body size (Fig. 7 c and d). The resulting ratio of work:energy can be as high as 73 % in larger animals and as low as 7 % in smaller animals. Energy input also increases linearly with speed, but at a faster rate in larger animals, while work output increases curvilinearly with speed, but at a slower rate in small animals (Fig 7 e and f)(Taylor *et al.* 1982, Heglund *et al.* 1982b). Therefore, animals seem to use energy more efficiently at higher speeds and when they are bigger (Fig. 7 g and h). If all muscles perform the same, how can these patterns be so?

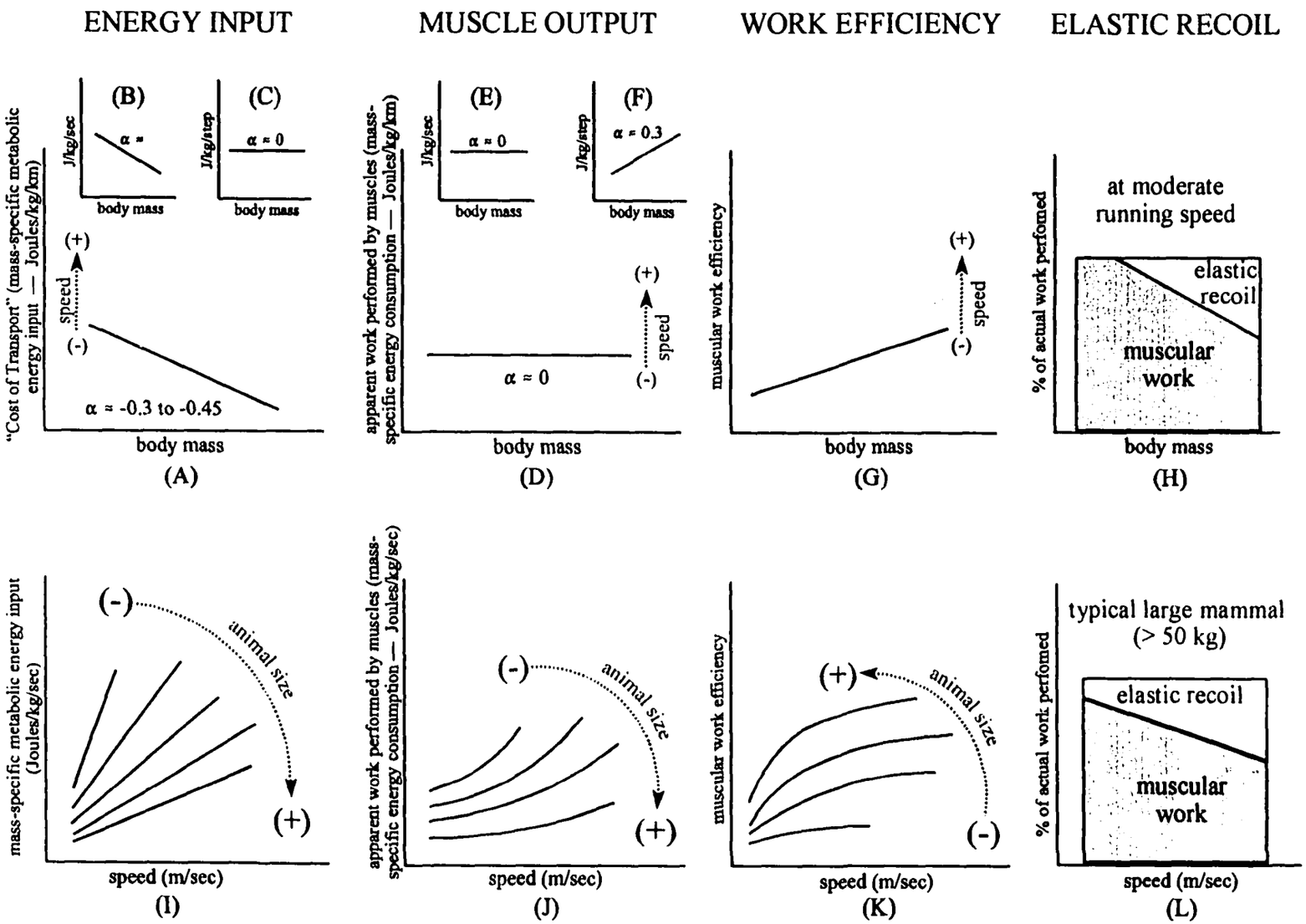
The explanation lies in the differing abilities of animals to store and recover elastic strain energy using tendons of the limbs— there is no intrinsic difference in muscle performance. The importance of elastic strain energy in the energetics of locomotion is becoming increasingly apparent, but evidently it only can be effectively used by large animals and/or at higher speeds, thus explaining the body size patterns observed in Fig. 7 (elastic energy also is important for hopping animals) (Cavagna *et al.* 1964, 1977a; Biewener *et al.* 1981; Alexander *et al.* 1982; Alexander and Bennet-Clark 1977; Alexander 1988, 1989; Heglund *et al.* 1982b; Heglund and Cavagna 1985; Bennett and Taylor 1995). The amount of energy stored in a tendon is a function of the distance stretched, and since tendons stretch as a percentage

Figure 7. Patterns of energy input and work output during locomotion showing how energetic efficiency increases with body size and with speed in larger mammals, due to their increased ability to recoil elastic strain energy stored in leg tendons.

Body Mass (top row): The energy expended to move one kg of body mass over 1 km (cost of transport) decreases in larger animals (*A*). While smaller animals spend energy at a faster rate (per kg) (*B*), all animals spend about the same amount of energy per kg per step (*C*)— smaller animals simply need to take more steps to move 1 km, and thus spend more energy doing so. However, the mass-specific work performed by the muscles to move 1 km does not increase with size (*D*), meaning that work efficiency (work performed : energy input) increases with body size (Values in *G* are per km efficiency derived as the ratio of *D* : *A*. Similar patterns arise from comparing *E* : *B* and *F* : *C* for work performed per second and per step respectively). But actual performance of muscle fibers does not vary among mammals and the increased efficiency of larger mammals arises because they are able to store and recoil more elastic strain energy. *H* shows how the smallest mammals recover almost no elastic energy even when running, while this energy may account for nearly 50 % of the work performed in very large animals.

Speed (bottom row): Mass-specific rates of total metabolic energy consumption increase linearly with speed, but at slower rates in larger mammals (*I*), but the energy used by the muscles to perform work increases curvilinearly and at slower overall rates in larger mammals (*J*). Thus, work efficiency also increases with speed (*K*) because the amount of kinetic energy stored and recovered as elastic strain energy increases with speed. This effect is amplified as animals get larger, as depicted in *L* for a typical large courser (this pattern also is apparent from the dotted lines in upper graphs). (Data compiled mostly from Taylor *et al.* (1970, 1982) and Heglund *et al.* (1982b). α = slope; scales are logarithmic)

Large size and speed increase locomotor efficiency because both increase vertical ground forces imparted to the limbs— these are the forces that stretch leg tendons and become available as stored elastic strain energy. Large size (or long legs) also increases the potential use of elastic strain energy because a tendon's ability to stretch is dependent on its length, which generally increases with body size. These patterns of energetic efficiency mean that *Arctodus*' large size and elongated legs allowed it to recover considerable elastic strain energy during locomotion, even at low speeds. For reasons discussed in the text, *Arctodus* probably rarely ran at high speeds, so its limb morphology strongly suggests that it had evolved for super-efficient moderate speed travel.



of their length, long tendons store more energy. It takes fairly high forces to stretch a tendon, such as the forces generated at high speeds. But higher force also can be generated by increasing mechanical advantage to the tendon or by increasing the applied mass.

For these reasons, elastic storage can be used by large animals even at modest speeds, whereas medium-size mammals only store elastic energy while running at faster speeds. The camel stores a considerable amount of elastic energy even at moderate speeds because it has super-long tendons with high mechanical advantage, which are stretched simply by the animal's weight and minimal dynamic forces (conclusion extrapolated from data in Alexander *et al.* 1982). This is an important point, because it shows how very large mammals with long legs are optimized to store elastic strain energy even at lower speeds. Apparently, the tendons of small animals are too stiff and too short to store significant amounts of elastic strain energy and small animals generate less absolute force during locomotion. Also, in order to store elastic energy, tendons must comprise a considerable percentage of the muscle/tendon length (Alexander 1992). In small mammals, most of this length is comprised of muscle (Alexander *et al.* 1981, 1982; Biewener *et al.* 1981).

Tests on *in vitro* tendons show they can return up to 93 % of stored energy as elastic recoil, while only 7 % is lost as heat (Ker 1981). In running animals of moderate size, up to ≈ 50 % of the work performed during each stride can be derived from elastic recoil of energy stored in tendons, but average recovery is more like 35 % (Cavagna 1964, 1977a; Alexander and Bennet-Clark 1977; Ker 1981; Alexander *et al.* 1982; Heglund *et al.* 1982b; Taylor 1985). It is likely that the disparity between work efficiencies in large and small animals described earlier (Fig. 7) can be largely attributed to their differing abilities to store elastic strain energy. However, Heglund *et al.* (1982b) suggest another compelling reason for the difference: because small animals take more steps at a given speed, they must generate forces for locomotion at higher rates and consequently they have a higher percentage of fast-twitch muscle fibers. Fast-contracting muscles generate force at reduced efficiency, perhaps explaining some of the reduced work efficiency of small animals.

McMahon (1975b, 1977, 1985) developed a theory to describe animal locomotion based on the mechanics of spring models and stored elastic energy. He proposed that most of the actual energy consumed by muscles at steady state running speeds does not result in muscle shortening (technically, no work is performed), but rather is used isometrically to keep the springs (tendons) under tension. Under this theory, a high percentage of the energy exchanged during steady state locomotion is mediated through spring oscillations. Furthermore, the theory predicts that animal limbs, like springs, should oscillate at natural harmonic frequencies that depend on size, which will dictate optimal steady state speeds for each gait (natural speeds, not maximum speeds). In fact, Taylor (1985) showed that for any given gait, there is an optimal speed (limb frequency) that maximizes the amount of recovered elastic strain energy. If an

animal runs below that frequency (too slow), the strain dissipates as heat; if it travels above that frequency (too fast) there is not enough time for the tendon to stretch or for the foot to apply the tendon's force. This is another reason why small animals are not able to utilize much elastic strain energy— because they naturally have greater stride rates and thus swing their limbs at higher frequencies. McMahon's model is consistent with the findings of Taylor *et al.* (1980), who showed that a great deal of energy consumed by muscles is used isometrically and during muscle stretch to control motion at the joints and to maintain posture.

Optimal Speeds Within a Gait and the Effect of Limb Length— Reconsidering the Cost of Transport

Hoyt and Taylor (1981) measured oxygen consumption in horses that were trained to extend their gaits (walk, trot, gallop) to speeds above and below those normally used within each gait (Fig. 8). Through this manipulation they were able to show that energy consumption increases curvilinearly with speed for each gait, and that horses change gait where these lines intersect (Fig. 8a). Furthermore, there is an optimal speed for each gait which minimizes the energy expended to move a given distance. When allowed to move at natural speeds, the animals chose these optimal speeds with little variance (Fig. 8b). Pennycuick (1975) also observed that wild African bovids choose a very narrow range of speeds within a gait. Hoyt and Taylor's data further show that the minimum cost to move a given distance is the same for a walk, trot, or gallop— that is, cost of travel (per km) is independent of speed. Later, Kram and Taylor (1990) reasoned that this is because the cost of transport is inversely proportional to step length, and while an animal may expend energy faster at higher speeds, the increased efficiency of longer strides at higher speeds balances this out, yielding no net change in the cost of transport.

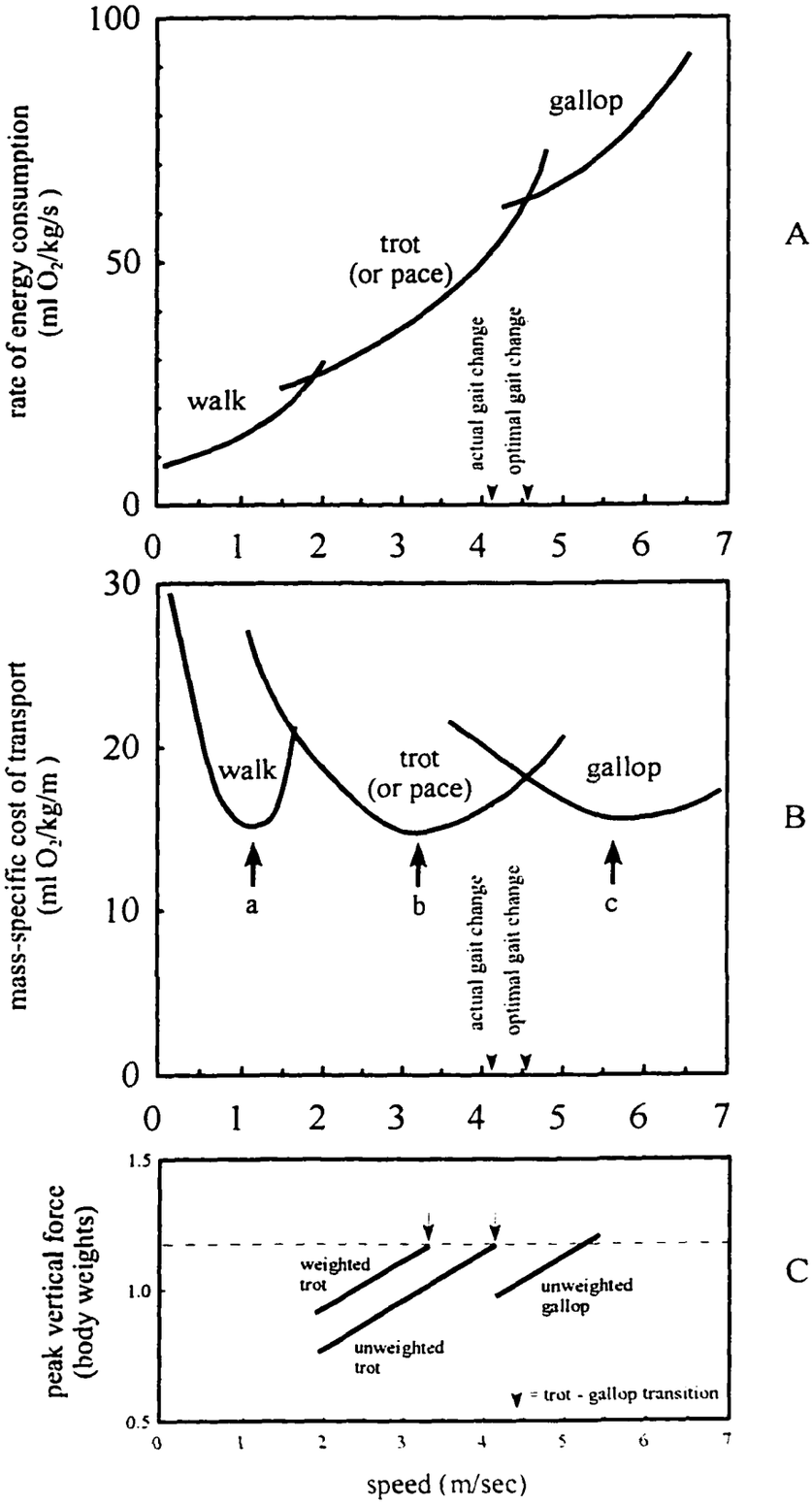
The study by Kram and Taylor (1990) revealed another important pattern relating limb length to the cost of transport. Consider the fact that as running animals increase speed, their feet contact the ground for a shorter percentage of the stride (i.e., there is a longer aerial phase), yet the magnitude of vertical ground forces increases. Since the feet have less time to distribute these forces at higher speeds, the mass-specific rate and magnitude of force application to the limbs naturally increases with speed (Cavagna *et al.* 1977a, 1977b). Kram and Taylor (1990) showed that the mass-specific rate of energy consumption is inversely proportional to the mass-specific rate of force application, i.e., energy is saved by applying force more slowly. This means that animals which spread the forces of locomotion over a greater time spend less energy on locomotion. Now consider the following relationship:

$$V_g = L_c \quad t_c \tag{5}$$

where V_g is ground speed, L_c is step length, and t_c is the time each foot is on the ground. Since step length

Figure 8. Patterns of energy use and force application across gait transitions in large mammals. *A* and *B* are modified from Hoyt and Taylor (1981) who measured energy consumption in small horses ($\bar{x}$ mass = 140 kg) that were trained to extend their gaits beyond normal speeds. Rates of energy expenditure increase curvilinearly with speed within each gait (*A*), but when animals are allowed to choose their own steady state speeds they use speeds that are energetically optimal for each gait (points *a*, *b*, and *c* for walking, trotting, and galloping in *B*). Also note from *B* that the cost of moving a given distance (the mass-specific cost of transport) is essentially independent of speed or gait at these optimal points (only rate of energy consumption varies). Since gait transitions occur below optimal speeds (where lines cross) they must not be triggered directly by energetics. *C* depicts Farley and Taylor's (1991) data on horses that ran carrying extra weights, showing that gait transitions seem to be triggered when critical levels of vertical ground force (limb stress) are reached, since animals carrying extra weight changed gaits at lower speeds.

Curves in *A* and *B* shift to the right with increasing body size, so larger animals will naturally walk, trot (or pace), or gallop at higher speeds. However, top galloping speeds appear to be limited by critical levels of limb stress, as in *C*. The dynamic forces of locomotion increase with body size at a faster rate than animals can increase skeletal strength, so critical force levels are reached at lower speeds in very large animals (also see Fig. 10).



is directly related to leg length, it is apparent that, at any given speed, long legs will be in contact with the ground for longer periods than short legs. *As step length (i.e., leg length) increases, the time course of force application increases and the cost of transport goes down proportionately.* (Later I will show that this pattern arises because muscles use energy more efficiently when they contract more slowly— that is, when their force is applied over a longer period of time.) Larger animals have relatively longer legs and take longer strides, and their step length increases like other linear dimensions, roughly proportional to $m^{0.3}$ (Kram and Taylor 1990). Because larger animals have longer legs, this helps explain why they have a lower cost of transport and why this cost can be reduced in any animal just by increasing leg length. Furthermore, since smaller animals run at higher stride rates and take more steps per kilometer, they consume energy faster at all speeds. These are important relationships that I will return to repeatedly, as they clearly have implication for *Arctodus*.

As I move into the next sections, I will be discussing locomotion less from the viewpoint of physiologists and more from the viewpoint of morphologists. There are a couple of reasons for this. First, most physiological studies measure locomotor energetics on animals in steady state locomotion— that is, animals traveling at constant speeds (no acceleration or deceleration), constant direction (no turning), and for short periods (no fatigue). These conditions are not typical for wild animals, especially carnivores, so the data is not always relevant in terms of evaluating real-world performance limits. In particular, these studies reveal little about the mechanics of acceleration and anaerobic contributions to locomotion— two important issues for an animal suspected of being a predator.

Furthermore, data from locomotor physiologists explain some of the energetic advantages and disadvantageous of animal size, but they have done a poor job explaining the finer details of limb design, and in particular, how animals built for long distance running differ from those built for sprinting (for instance, see Taylor *et al.* (1974), whose data show that the cost of running is the same in a cheetah, gazelle, and goat). The next three sections address these types of questions. First I examine the way muscles generate force and bones dissipate these forces, and how such variables depend on body size and limb configuration. Then I evaluate limbs as lever systems and discuss the concepts of mechanical advantage and high gear/low gear muscles. The final section is a discussion of kinematics and the way that mass distribution affects the performance of limbs.

7. Scaling of Muscle Force

I mentioned earlier that the performance of individual muscle fibers remains essentially constant across mammalian taxa. However, in order to understand the specific ways that locomotor performance is impacted by relative body size and limb morphology, it is important to consider how size influences a

muscle's capacity to generate *force*, *power*, and *work*.

Force: The force generated by a whole muscle is a function of the number of fibers contracting, which is proportional to a muscle's cross-sectional area (Hill 1950; Alexander 1977a, 1992). Regardless of the scaling scheme, cross-sectional area functions are predicted to increase with body size at a slower rate than mass or volume functions ($m^{2/3}$ under geometric scaling). Therefore, one might expect that, as animals get larger, they will have increasing difficulty generating the forces necessary to move their own masses. It turns out that cross-sectional area and force generation in limb muscles scale around $m^{0.8}$, not $m^{2/3}$ (Alexander *et al.* 1981), and for reasons I discuss later, locomotion in large animals is not limited by their ability to generate adequate force.

Work: The work ($W = F \cdot d$) performed by a muscle equals its force output (cross-sectional area) times its shortening distance, which is about one third of its total length (Hill 1950). This calculation (cross-sectional area x length) makes work output a function of muscle volume, and thus isometric with body mass (work $\propto m^{1.0}$) (Alexander 1977a). Therefore, work output is predicted to keep pace with changes in body size. Previously I mentioned that muscle fibers generally convert metabolic energy into mechanical work at about 25 % efficiency, but that recorded efficiencies are much higher in larger animals and running animals. I also showed that this "extra work" is performed by elastic strain energy stored in tendons, which can theoretically return up to 93 % of stored strain energy to perform work (Ker 1981). While total work performed indicates something about energetics and metabolic efficiencies, it is not always a very useful way to judge locomotor performance because it is not time specific— that is, when an animal moves a given mass over a given distance the amount of work performed is the same, whether it takes a minute or a day.

Power: To evaluate features such as speed and acceleration, it is more useful to think in terms of the rate that work is performed or the velocity of force application— this is *power* (P):

$$P = W / t = F \cdot v \qquad (6)$$

where W is work, t is time, F is force, and v is velocity. Power is a function of the velocity that a muscle contracts in relation to the amount of work being done. For comparison, a muscle's strength is measured by its capacity for work, but power is a measure of how fast it does that work— strength does not equal power. Powerful muscles are energetically inefficient because muscles consume energy at a rate that is directly proportional to the forces they exert (Taylor *et al.* 1980) and because fast muscles use energy at disproportionately high rates (i.e., they are less economical) (Alexander 1973, 1992). But fast muscles also produce less force and empirical data show that muscle economy is almost doubled by cutting the speed of contraction in half (Huxley 1974, Heglund and Cavagna 1985, Alexanders 1992).

Histologically, fast muscles are less efficient because actin-myosin crossbridges dissociate more rapidly, before each has completed a full shortening cycle. Also, crossbridges form and dissociate so quickly that they do not always pull in unison— some may be shortening the filament while others have not released, and so are resisting shortening (Close 1972, Heglund *et al.* 1982b, Alexander 1992). This also explains why fast-contracting muscles generate less force, and why slower, longer muscles are more energy-efficient and generate higher forces (but more slowly— i.e., with less power). The rate of muscle contraction also is inversely proportional to muscle length, so long muscles inherently contract more slowly, generating more force but less power than short muscles. This is because long muscles have more filaments shortening simultaneously, and crossbridges do not need to form and dissociate as frequently as in short muscles while generating equivalent forces. There also is evidence that pumping Ca^{+} across cell membranes (the trigger for a muscle twitch) may consume up to 30 % of the energy used by muscles (Homsher *et al.* 1972). Since this trigger fires more frequently in fast muscles, it increases their rate of energy consumption. Therefore, powerful muscles must be both fast (short) and strong (large cross-sectional area). Later, I will show that the power generated by a muscle also depends on the limb's mechanical advantage.

The power output of a muscle depends on muscle size and speed of contraction, but ultimately it depends on muscle loading— the other end of the equation— which varies considerably among animals of different builds. Muscle loading is equivalent in magnitude to the tensile forces resisting a muscle during contraction, so it is a function of the mass being moved relative to the force exerted and the muscle's mechanical advantage (mechanical advantage is explained in the next section). Heavily loaded muscles require more force to contract, but in order to generate these forces they naturally contract more slowly, which reduces power. Later I will show that this is the type of muscle found in the limbs of animals such as tortoises and fossorial mammals (diggers). These animals have heavily loaded limbs that do a lot of work, but slowly. Thus, they are strong, not powerful, animals. Animals that rely on acceleration have powerful limb muscles, because they need to bring their limbs up to maximum velocity as quickly as possible. Therefore, the muscles of a good accelerator should have reduced loading, while muscle force, size, and mechanical advantage should be maximized. This formula predicts certain builds in a good accelerator: muscle mass should scale positively with body mass, and as mentioned above, muscles should be wide (to generate high force) but short (for quick contractions). The remainder of this section on muscles uses published data to test each of these predictions.

Muscle Mass: If mammalian muscles scale geometrically, one would expect muscle mass to increase $\propto m^{1.0}$. In fact, the empirical value is very near this when all mammalian taxa are averaged (Alexander *et al.* 1981, Calder 1984). But I want to determine if powerfully-built mammals deviate from this average. Alexander *et al.* (1981) measured the mass, length, and cross-sectional area of limb muscles

in relation to body mass in numerous mammals. Unfortunately these authors pooled their data into a few broad groups based on taxa, not locomotor style. For instance, they combined data for all Carnivora, including diverse forms ranging from ferrets and mongooses to lions and hyenas. However, their data still show that muscle mass in carnivores scales higher than other mammals for almost all muscles measured (Table 3). The scaling factor for carnivores varies by muscle and is between $m^{1.02}$ and $m^{1.23}$, with an average of $m^{1.12}$. Averages for bovids and primates are $m^{1.02}$ and $m^{1.07}$, respectively. Calder (1984) compared actual muscle mass in mammals versus values predicted by general allometric equations. He showed that in dogs (the only carnivore he analyzed) actual muscle mass is 1.24 times greater than the predicted value. Values for horse (*Equus caballus*), deer (*Odocoileus virginianus*), and wapiti (*Cervus elaphus*) are 1.14, 1.00, and 0.98 respectively. Davis (1962) measured muscle mass in lions and found it to constitute up to 62.5 % of body mass— the highest amongst mammals. The average range for mammals is about 44 - 50 % (Pitts and Bullard 1968, Munro 1969, Calder 1984). Values for other felids are between 56 - 59 % (Munro 1969, Calder 1984).

Muscle Force: Under predictions of geometric scaling, muscle force should increase with body size as a function of their cross-sectional area, or $m^{2/3}$. However, Alexander's (Alexander *et al.* 1981, Alexander 1985) empirical data on muscle cross-sectional area indicate that muscle forces scale more like $m^{0.8}$. Alexander arrived at this value for cross-sectional area by measuring muscle mass ($m^{1.1}$) and fiber length ($m^{0.3}$) in numerous mammals, and dividing the former by the latter ($m^{1.1} \div m^{0.3} = m^{0.8}$). These values are for proximal limb muscles, but values for distal muscles are similar. The authors also suggest that the actual scaling of muscle may be closer to $m^{0.9}$). This value, although higher than predicted by geometric scaling theory, is not surprising, since 2/3 scaling would cause muscle force to lag well behind the mass it must move. One might conclude that even $m^{0.8}$ (or $m^{0.9}$) scaling means that muscle force is not keeping pace with body mass, but consider the following: Alexander *et al.* (1981) calculated that if limb muscles generate maximum forces proportional to $m^{0.8}$, but their moment arms scale as $m^{0.4}$ (moment arms are discussed in section 7), then the maximum bending forces generated by these muscles will be $m^{0.8} \times m^{0.4} = m^{1.2}$. In other words, bending forces increase faster than body mass. It will be shown below that leg bones can withstand bending moments that are related to the cube of their diameter[5]. Bone diameter scales as $m^{0.36}$, so withstandable bending moments scale as $m^{1.08}$ (the result of cubing $m^{0.36}$). *These calculations show that the force generated by limb muscles ($m^{1.2}$) is theoretically greater than the bending strength of limbs they move ($m^{1.08}$), and that large animals should not be fundamentally limited by the forces generated in their muscles.*

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[5] the bending moment of a bone is equal to its cross-sectional area times its length. Since $S.I. = l^2$, the bending moment is equivalent to $S.I. \times l$, or l^3.

TABLE 3. Scaling dimensions in mammalian limb muscles. All values are scaling exponents (α) derived from the allometric equation $y = bm^{\alpha}$, where m is body mass. Mass and length data (first two columns) from Alexander *et al.* (1981), last two columns calculated using those authors' data.[1]

muscle group	exponent of muscle mass	exponent of muscle fiber length	exponent of muscle cross-sectional area (mass ÷ length)	bulkiness index (S.A. ÷ length)
Adductor & Hamstrings				
primates	1.06	0.26	0.80	0.54
carnivores	1.18	0.37	0.81	0.44
bovids	0.97	0.19	0.78	0.59
others	1.10	0.27	0.83	0.56
Quadriceps				
primates	0.99	0.39	0.60	0.21
carnivores	1.16	0.42	0.74	0.32
bovids	0.94	0.25	0.69	0.44
others	1.08	0.32	0.76	0.44
Ankle Extensors				
primates	1.12	0.30	0.82	0.52
carnivores	1.02	0.16	0.86	0.70
bovids	0.97	0.23	0.74	0.51
others	0.97	0.14	0.83	0.69
Deep Hind Flexors				
primates	0.76	0.16	0.60	0.44
carnivores	1.03	0.24	0.79	0.55
bovids	1.03	0.18	0.85	0.67
others	1.01	0.20	0.81	0.61
Triceps				
primates	1.27	0.36	0.91	0.55
carnivores	1.23	0.33	0.90	0.57
bovids	1.10	0.30	0.80	0.50
others	1.11	0.33	0.78	0.45
Fore Flexors				
primates	1.19	0.38	0.81	0.43
carnivores	1.11	0.24	0.87	0.63
bovids	1.09	0.33	0.76	0.43
others	1.04	0.18	0.86	0.68

[1] All values are exponents so division is by subtraction

With those principles in mind, I still want to test the prediction that powerful animals and good accelerators will have limb muscles with relatively greater cross-sectional areas (forces). Table 3 contains Alexander *et al.'s* (1981) scaling exponents for muscle mass and fiber length for six limb muscles in primates, fissiped carnivores, and bovids. I have divided the masses of these muscles by their lengths in order to calculate their cross-sectional areas. Cross-sectional area estimates the force generated by a muscle. Results of these calculations (Table 3, column 4) show that fissiped carnivores have the highest force values for nearly all muscle groups. The higher value for triceps in primates is to be expected because of their specialized locomotion (the group includes brachiators). Values for cross-sectional areas of the deep hind flexors are highest in bovids, but these are a minor group of muscles that mainly flex the digits and are expected to be larger in bovids because they have greatly elongated metapodials.

Muscle Length: The comparison gets more difficult when one considers relative muscle lengths in mammals (which I predicted to be relatively shorter in good accelerators). This is because most ungulates reduce (shorten) the muscle portion of a muscle-tendon unit, effectively increasing the tendon portion so that more elastic strain energy can be recovered (Alexander 1977a, 1984; Alexander *et al.* 1981, 1982). So, in comparison, the muscles fibers of large carnivores and other powerfully built animals seem long, apparently contradicting my prediction. To address this problem, I have calculated a "bulkiness index" by dividing cross-sectional area by fiber length (Table 3, column 5). This index gives an indication of a muscle's relative width versus length (i.e., its bulkiness). Muscles with long stretch tendons in bovids have higher bulkiness indices because these muscles have reduced lengths, not greater widths. These include the hamstrings, deep hind flexors, and the quadriceps (the quadriceps both extend the knee and flex the thigh; the extensor portions can store elastic strain energy and have longer ligamentous portions). For all other muscles, the more powerfully built carnivores and primates have bulkier muscles— that is, shorter for quickness, and wider for high force generation.

Powerful Limbs vs. Efficient Limbs: So far, I only have discussed muscles designed for high power output. However, mammals vary considerably in muscle configuration, balancing needs for power and efficiency; some emphasize sustained work, while others emphasize sustained high speeds. I showed that powerful muscles fatigue quickly because they contract rapidly and are short. Muscles built for economy have the opposite traits. They are long and narrow to provide slower, more efficient contractions. Animals with these types of muscle that also develop high top speeds do so by decreasing the mechanical advantage of their limbs, which effectively increases their turning velocities but reduces their strength. In the next section on lever systems, it will become apparent that this separates runners with high top speeds from those that simply accelerate well. And in fact, this is what drives the differences in muscle proportions among the carnivores and bovids in Table 3.

With *Arctodus'* long legs, it stands to reason that either its muscles were longer and/or it had

long stretch tendons. Considering the muscle anatomy of bears, it seems unlikely that *Arctodus* had evolved elaborate stretch tendons like ungulates. But even in running humans, not known for their stretch tendons, about one third of the work performed during running comes from recovered elastic strain energy, and any large, long-legged mammal will use a good deal of recoiled elastic energy during locomotion (Alexander 1988, 1992; Alexander and Bennet-Clark 1977; Alexander *et al.* 1982). Another important implication of *Arctodus*' long legs is that the accompanying elongated muscles would have been optimal for slow, repeated contractions, and/or high force (but not power) generation; in a very large animal, this would be most adaptive for efficient and sustained locomotion, not for power and acceleration. I also have been alluding to the probability that the long, slender legs of such a large animal could not have withstood the strains of sudden turns, rapid speed changes, or high speeds that characterize almost all modes of predation. To understand why this is so, one needs to consider how bone strength scales with body size and how this affects a bone's ability to incur the forces of locomotion. I address those issues next.

8. Bones and Skeletal Stresses

As the primary elements of rigid support, bones incur both the static forces of supporting an animal's mass and the greater dynamic forces of locomotion. In this section, I will discuss how *both the static and dynamic forces of support increase with body size at rates faster than skeletal strength, and that this scaling effect ultimately limits animal locomotion.*

Forces, or loads, incurred by bone are transmitted internally as stresses (see definitions section) and are dissipated as deformational *strains*, usually as bending, compressive, torsional, shear, and tensile strains (tensile strains are not significant in bones, but they are the main strains incurred by muscles and tendons). A bone's *strength* is a measure of its ability to deform under stress without breakage or permanent deformation, and a bone will break when stresses exceed its deformational capacity— i.e., its strain limits. For almost all limb bones (with exceptions such as metapodials in ungulates) bending forces are by far the most important stress threatening a bone's integrity— typically 80 - 90 % of the stress in a bone is from bending; the balance is usually compressive stress (Rubin and Lanyon 1982, Biewener *et al.* 1988). When a bone yields to bending stresses it is said to *buckle*. A bone's *safety factor*, or safety margin, is the ratio between its normal strain and its yield strain. Typically, bones which incur mainly compressive stresses are straight, while those incurring mainly bending stresses are curved. Curved bones are less resistant to bending stresses, so this pattern seems odd at first. However, the axis of curvature is invariably in line with the normal direction of bending, and it has been suggested that this curvature is "predictive," focusing bone strain in a single direction, which then can be countered by strategic

remodeling (Rubin and Lanyon 1985, Biewener *et al.* 1988). This strategy conserves materials since the bone does not need to be built to resist bending in other directions.

Predicted vs. Actual Bone Stress

Here I want to briefly describe how dimensional analyses of limb bones predict that larger animals will incur greater dynamic forces in their bones, whereas the actual data on bone stress show that they do not.

A bone's strength is a function of its dimensions and thus is subject to scaling influences. Compressive, torsional, and shear *strength* are primarily related to a bone's cross-sectional area, which would be proportional to l^2 and $m^{2/3}$ if animals were built in a geometrically similar fashion (recall l is any linear dimension, including bone diameter, and $l \propto m^{1/3}$ in geometrically similar animals). On the other hand, the magnitude of compressional, torsional, and shear *forces* acting on bone should be a function of body size (i.e., m^1 or l^3), in geometrically similar animals. Therefore, it would be surprising if large mammals actually scale geometrically; otherwise, how could they withstand the forces of running? Alexander *et al.* (1979) measured limb bone dimensions and found that most mammalian limbs bones do in fact scale close to geometric proportions (except in bovids). Specifically, these authors found that long bone diameters (d) are generally proportional to $m^{0.36}$ — slightly, but not significantly, higher than $m^{1/3}$ (they also found that $l \propto d^{0.97}$, in accordance with geometric proportions, except in bovids). Using Alexander *et al.*'s data, cross-sectional area (d^2) thus scales empirically as $m^{0.72}$ (the square of $m^{0.36}$), which is statistically indistinguishable from geometric prediction of $d^2 \propto m^{2/3}$ (statistical analysis by Alexander *et al.* 1977). This implies that the compressional, torsional, and shear strength of bone should increase with body size only as $m^{0.72}$, meaning that stresses will still increase as $m^{0.28}$ (i.e., as $m^{1.0} - m^{0.72}$) (the same value was predicted by Biewener 1982). In other words, larger animals are predicted to incur relatively greater compressional, shear, and torsional stresses in their limb bones than smaller animals.

Similarly, bending strength, the most critical factor determining dynamic bone strength, is a function of a bone's cross-sectional area times its length. Under rules of geometric similarity bending strength is predicted to scale as $d^2(l) = l^3 = m^{1.0}$. Using Alexander *et al.*'s empirical data for bone diameter (see above), actual limb bone bending strength would appear to scale closer to $(d^{0.36})^3$, or $m^{1.08}$. However, Alexander *et al.* (1981) subsequently calculated the theoretical maximum bending moments generated in limb muscles by multiplying their cross-sectional area ($\propto m^{0.8}$) times their moment arm ($\propto m^{0.4}$), yielding bending forces $\propto m^{1.2}$ (see previous section on muscle scaling). If maximum bending moments of limb muscles increase with body size $\propto m^{1.2}$, but bending strength of limb bones increases only $\propto m^{1.08}$, then one would predict that bending stresses also will increase disproportionately with body size at a rate or increase $\propto m^{0.12}$ ($m^{1.2} - m^{1.08}$). Biewener (1982) predicted this value to be $m^{0.28}$, identical

to the prediction above for increases in compressional and shear stresses.[6]

When dynamic stresses are actually measured in bones, it is apparent that the mass-specific magnitude of these stresses is fairly independent of body size (proportional to m^{0}) in animals running at physiologically equivalent speeds, such as at gait transitions or at maximum speeds. In fact, this is just what Alexander (1977a) initially predicted when formulating his theory of dynamic similarity (also see Alexander and Jayes 1983). Not only are dynamic stresses independent of mass (i.e., not $\propto m^{0.28}$ or $m^{0.12}$), but all mammals locomote within about the same safety factor in their bones — around 2.1 - 3.1 (Alexander 1977c, Alexander *et al.* 1981, Alexander and Jayes 1983, Rubin and Lanyon 1982, Biewener 1983b, Biewener and Taylor 1986, Biewener *et al.* 1988, Kram and Taylor 1990). Figure 9 (modified from Biewener 1982) depicts the absolute bending strength of bone measured in a variety of sizes of mammals and shows how this value does not change significantly with body size. Figure 9 also shows the way that absolute bone strength would need to increase with body size in mammals if dynamic stresses increased with body size $\propto m^{0.28}$ — the value predicted by strictly dimensional analyses.

How do Large Animals Reduce Realized Bone Stress?

The reason why actual stresses in bone scale as m^{0} is important: *the physical dimensions of large and small mammals may scale roughly according to geometric predictions, but large and small animals do not run in geometrically similar ways.* Large animals decrease the realized stresses of locomotion and maintain similar safety margins as do small animals by running much more conservatively (but not necessarily slower) and through modified limb architecture. By running more conservatively, I mean that large animals accelerate and decelerate at slower rates, and they avoid other sudden changes in velocity, such as those incurred during rapid turns. these are key principles that I will return to, but first I want to discuss the ways that large animals modify body architecture.

Architecturally, large animals reduce bone stress using three strategies: 1) reducing bone curvature, which scales as $m^{-0.09}$, 2) reducing angles of bone alignment, which scale as $m^{-0.07}$, and 3) reducing excursion angles, which scale as $m^{-0.1}$ (McMahon 1975a, Biewener 1983b). All of these strategies maximize axial loading (compressive forces) and reduce transverse loading (bending forces). Bone is more resistant to compressive forces than bending forces, and these three strategies reduce

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[6] These calculations, based purely on dimensional analyses, argue that mammalian limb bones scale geometrically and predict that larger animals should experience disproportionately greater static and dynamic stresses in their limb bones. I would qualify Alexander's conclusions, however, by pointing out that Biewener's (1983b) data on limb bone diameter and length across a broad range of taxa show that they scale as $l \propto d^{1.09}$, which Biewener reports as being significantly different from $l \propto d^{1.0}$. His data are combined for bovids and non-bovids, but his results can be taken to mean that mammals probably do increase bone diameter at a faster rate than bone length as body size increases in response to increased stresses

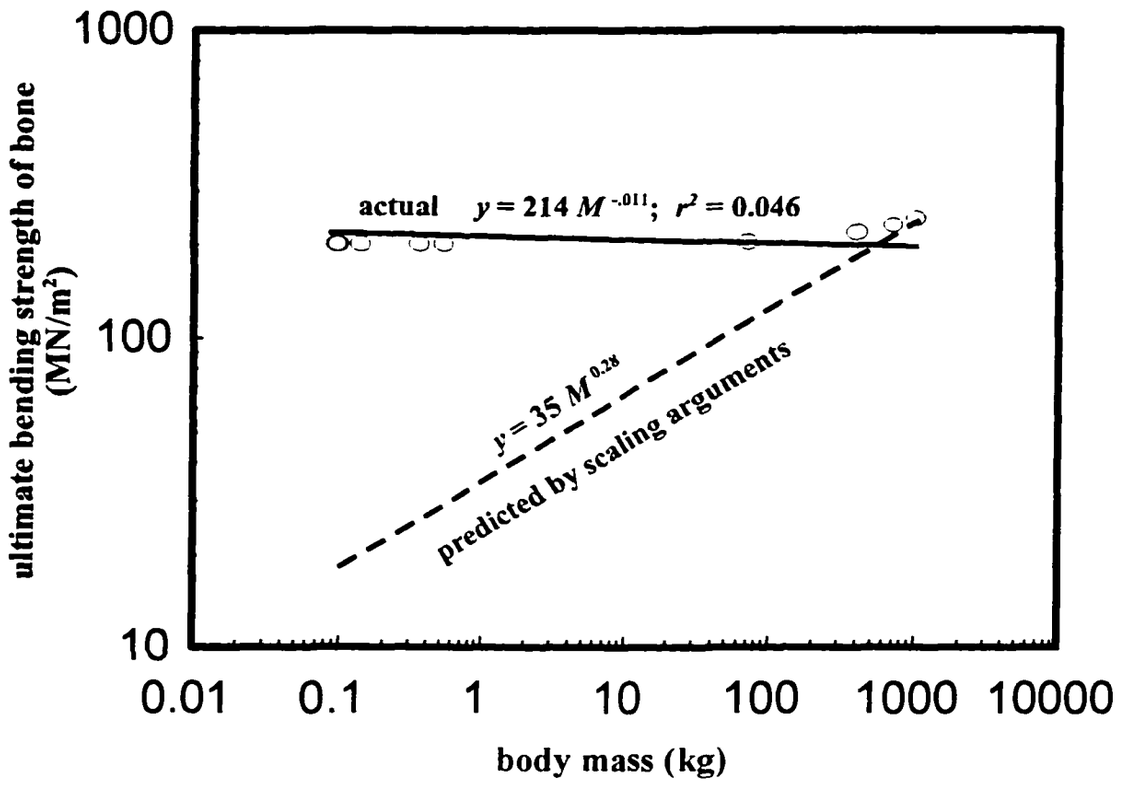

FIGURE 9. Actual bone strength in mammals (solid line) and the predicted bone strength that would be required if all mammals ran in geometrically similar ways and still maintained the same safety factor in their bones (dashed line). The slope of the line for actual bone strength is not significantly different from 0. The line for predicted bone strength was drawn using the actual bone strength in a 1000 kg animal and extrapolating backwards using a slope of 0.28 to derive a y-intercept value of 35. See text for derivation of slope. Adapted from Biewener (1982).

bending strains by keeping stresses more in line with vertical ground forces (Biewener 1983b, Biewener and Taylor 1986, Biewener *et al.* 1988). Thus, since curved limb bones generate greater bending moments, large mammals reduce bone curvature. Reducing the angle of alignment between bones keeps the limbs less bent at the joints. Reducing excursion angles makes the limbs swing through a smaller radius during locomotion.

While large animals stand and run with their legs less bent than small animals to reduce dynamic stresses, reducing joint angles has the additional effect of decreasing the mechanical advantage of muscles operating their limbs (levers and mechanical advantage are discussed in the next section). As a result, the straight-leg stance of larger animals generates less torque and imparts less stress to the bones than the bent-leg stance of smaller animals (Biewener 1983b). In the next section, I will discuss how reduced mechanical advantage is one reason why larger animals are less adept at acceleration. It is interesting to note, however, that the less curved limb bones of *Arctodus* have been interpreted as an indication of its cursorialism and running ability. Later, I will argue that *Arctodus* did in fact make many modifications to its limbs that were cursorial adaptations, but its straightened limb bones most likely reflect the greater stresses incurred by its large size and should not be strictly interpreted as a cursorial adaptation.

Previously, some authors (e.g., Pennycuick 1975, Alexander 1977b, 1977c) have suggested that large animals may be reducing bone strain by increasing duty factor. These authors reasoned that an animal can reduce the absolute magnitude of vertical ground forces and stress in the limbs by increasing the percentage of time that each foot contacts the ground during a stride, thereby spreading these forces over a longer period. For similar reasons, these authors predicted that duty factor also should increase with speed, since ground forces increase with speed (within a given gait). Pennycuick (1975) even suggested that ungulates change gaits for the purpose of increasing duty factor. Early data of Alexander's (1977b) seemed to support these hypotheses. He showed that duty factor is $\sim m^{0.11}$ for the front limbs of mammals and $m^{0.14}$ for their hind limbs. However, the hypothesis that duty factor increases with size or speed has largely been refuted. The data of McMahon (1977) and Biewener (1983b), for instance, show no increase in duty factor with either size or speed in quadrupedal mammals. Biewener's results even indicate that duty factor decreases curvilinearly with speed, and scales to body size with a slope not significantly different from zero (i.e., m^{0}). Later, Jayes and Alexander (1978) found that there is a drop in duty factor at the walk-trot transition, and that this increases leg loading. Subsequent studies have failed to show much change in duty factor at the transition from a trot to a gallop (McMahon 1977, Biewener 1983b, Rubin and Lanyon 1982, Kram and Taylor 1990).

Recent work has clarified the issue of force application by the feet, and shows that it is not a simple matter of changing duty factor. The pattern of force application depends on many complex and interdependent factors such as speed, gait, limb compliance, and leg length. Recall from the discussion of

energetics that the magnitude (and rate) of vertical ground force application increases with speed within a gait, but that it decreases again after a gait transition (for example, after switching from a trot to a gallop). The same pattern holds true for the rate of energy consumption (Hoyt and Taylor 1981)(Fig. 8a). These patterns hold true for animals of all sizes, but the rate of increase should be greater in small animals (recall Fig. 7). Next I want to return to Figure 8 and discuss these patterns in more detail.

When Hoyt and Taylor's (1981) data is plotted as the mass specific cost of transport (Fig. 8b), it can be seen that once an animal reaches a higher gait and is allowed to choose its own speed, it quickly settles on one that is the most economical for that gait, after which it consumes energy at about the same rate as it did during the previous gait. In Fig. 8b I showed that this steady state cost of transport is nearly the same for each gait, meaning that an animal expends about the same amount of energy to move a given distance regardless of its speed (only *rate* of energy consumption changes with speed— Fig. 8a). Furthermore, since the rate of energy consumption initially declines after a gait change, Hoyt and Taylor and others (Alexander *et al.* 1980, Alexander 1992, Hildebrand 1985a) have concluded that animals change gaits in order to save energy. This would be a correct conclusion if animals changed gaits at speeds where the lines in Fig. 8a and 8b cross. But this is not the case. Taylor's group (Farley and Taylor 1991) later measured energy expenditures in horses carrying various amounts of extra weight and showed that these animals change gaits at speeds below those which would optimize energy costs (speeds *a*, *b*, and *c* indicated on Fig. 8b). In other words, animals switch from a trot to a gallop at speeds where galloping actually requires more energy than trotting.

What Triggers Gait Changes— More Clues Into the Role of Body Size

If gait changes are not occurring at a speed that optimize energy expenditure, then they must be triggered by some other demand. There is good evidence from Taylor (1985), Biewener and Taylor (1986), and Farley and Taylor (1991) that animals change gait in response to threshold levels of musculoskeletal stress— that is, they change gaits when a critical level of stress is reached, regardless of speed. Almost universally, this point is reached when the bone safety margin (ratio of yield strain: applied strain) approaches 3 (Rubin and Lanyon 1982, Biewener and Taylor 1986, Biewener *et al.* 1988, Farley and Taylor 1991). This process is exemplified by Farley and Taylor's experiments with weighted-down horses. The weights increased limb loading and caused the animals to change gaits at subnormal speeds. However, while their speeds differed, the horses changed their gait when the same amount of critical vertical ground forces were reached. Biewener and Taylor (1986) also made a strong argument that *maximum speeds* in animals are defined by the strain limits of limb bones, not by an animal's ability to generate enough force or power (also see Taylor 1985 and next subsection).

But how is the rate of force application reduced by switching from a trot to a gallop? I indicated

that some earlier researchers hypothesized that animals reduce these forces by increasing duty factor, but this has been largely disproved. McMahon (1985) presented a compelling argument showing that galloping reduces leg strain by increasing leg compliance (a measure of leg stiffness). Stiff-legged (non-compliant) gaits like the trot and walk use less energy to flex and maintain bent limbs, whereby more of the work performed against the ground is converted to propulsion. For these reasons stiff-legged gaits use energy more efficiently than compliant gaits like the gallop. The tradeoff is that stiff legs transmit greater vertical ground forces, and because these forces increase with speed there is a rather low speed limit for stiff legged gaits (if safety margins are to be maintained).

Therefore, to dissipate increasing forces the legs need to become more compliant at faster speeds. The compliant legs of a gallop "absorb" the increased ground forces by flexing and then rebounding this energy as the feet are placed on the ground in rapid, non-overlapping succession, which also distributes the forces more evenly throughout the stride. The net effect is that peak vertical forces in the feet are reduced, step length increases, and the animal gets a smoother ride. McMahon's study shows that *compliant running consumes energy at a faster rate than stiff-legged running, but it is the only way to achieve higher speeds without exceeded the safety margins of limb bones.* Recall, too, the important conclusions of Kram and Taylor (1990), who show that longer legs decrease energy costs and decrease the magnitude of peak vertical forces (but not total force) imparted to the limbs because long legs afford an animal longer strides, longer individual foot contact, and thus more time to distribute these forces. Therefore, increasing leg compliance and leg length achieves all the hypothesized goals of increasing duty factor (and more), but without necessarily increasing the total period of foot contact with the ground (each foot spends a longer time on the ground in a gallop, but because there is a prolonged aerial phase, total foot contact as a percentage of the stride— i.e., duty factor— does not increase).

McMahon's data on compliant gaits provide critical insight into the *Arctodus* question in terms of gait selection. Recall that an animal uses the same amount of energy to move a given distance regardless of speed of travel— all that changes is the rate of energy consumption. But an animal cannot sustain maximum galloping speeds indefinitely because it is limited by the rate that it can provide energy to its muscles (Margaria *et al.* 1963, 1964). Combining this information with McMahon's data on rates of energy consumption during compliant and non-compliant gaits, one would predict that animals which can maintain non-compliant gaits at high speeds will have the fastest speeds of sustainable travel; they will use energy at a slower rate and get to far off destinations quicker, because they do not need to rest as often.

The inherently smoother ride of a compliant gait is not insignificant, as it reduces vertical displacement of the body's center of mass. Rubin and Lanyon (1982) showed that less displacement in a gallop (versus a trot) reduces limb loading when the body mass comes down on the feet. These authors also showed that the rate of strain change in a bone— not the magnitude of peak strain— often is the most

relevant factor determining bone strength. The stiff legs of a trot impart a much more rapid rate of strain change when the feet hit the ground than would the compliant legs of a gallop, which absorb vertical forces more gradually. Indeed, it was shown that this is probably why animals change gait (Taylor 1985, Biewener and Taylor 1986, Farley and Taylor 1991).

Not only are bones subject to failure from rapid strain change, but they also are prone to damage by rapidly repeated strain, or repetitive loading. This type of "fatigue damage" occurs because the bone is not allowed to recoil, or "de-strain." The accumulation of strain means that even low levels of stress can cause failure when applied constantly or in rapid succession (Rubin and Lanyon 1982). The pattern of bone breakage in mammals indicates that both fatigue strain and the rate of strain change can be more important than the magnitude of strain in causing bone failure. For example, The vast majority of fractures in steeplechase horses occur during jumps, both at takeoffs and landings (Currey 1981, Biewener *et al.* 1988). Those are times when limbs experience the most intense rate of strain change and their greatest rate of acceleration and deceleration; but the fractures probably occur in part because of fatigue strain accumulated during the course of the race.

Biewener (1983a) and Biewener *et al.* (1988) measured bending and compressive strain at different points along limb bones of running mammals (horses, dogs, chipmunks) and found that distal bones generally experience strains 1.5 to 2.0 times greater than proximal bones. This would suggest a strong evolutionary incentive to keep distal bones stout, yet these bones are highly reduced in many coursers (for reasons discussed in the section on kinematics).

A closer look at patterns in Biewener's strain data for the limbs of running horses shows that the tibia and radius receive the highest bending strain values, followed by both metapodials (receiving predominantly compressive strains). But data on bone breakage in horses show that metatarsals are fractured much more frequently than tibias (Currey 1981). Biewener (1983a) argued that this apparent discrepancy arises because strain is typically measured in animals running at a steady state, while bone breakage occurs during brief periods of extreme stress, concurring with Rubin and Lanyon's (1982) data. When Biewener (1983b) measured bone strain in a small mammal (chipmunk, *Tamias striatus*), he found that its metatarsals incur greater strains than its tibias. Small animals normally run with relatively greater acceleration, greater rates of force application, and greater stride rates compared to large animals, so small animals routinely experience more rapid changes in strains, more accumulated fatigue strain, as well as greater peak strains than large animals. Therefore, Biewener argues that these data on a small mammal more accurately assess bone strain during strenuous locomotion such as during rapid acceleration/deceleration and that these are the critical tests of bone strength. Hence, during rigorous running, a horse's metatarsal, not its tibia, probably experiences the most strain, which the studies of steady state locomotion could not demonstrate.

An Upper Size Limit For Predators

Throughout this discussion, I have been alluding to the notion that the scaling of locomotor forces sets an upper body size limit for conventional predators— somewhere in the neighborhood 250 kg. At this point I want to examine this hypothesis more closely and present what may be an important new empirical relationship between maximum running speeds (MRS) and body size. This discussion closely follows Fig. 10.

Figure 10a reconstructs Garland's (1983, Fig. 1) data relating MRS to body size across a wide range of mammalian taxa, from shrews to elephants (Garland's data for the smallest mammals has been cropped out of Fig. 10a). The polynomial fit to these data ($log\ MRS = 1.47832 - .025892\ (log\ Mass) - 0.06237\ (log\ Mass)^2$; $r^2 = 0.574$) shows how MRS increases with size but plateaus around 119 kg, after which it clearly drops off with increasing body size. The physical and biological forces driving this pattern have been discussed throughout this chapter, but only in a qualitative sense. In Fig. 10b, I propose a quantitative reason for it. This plot shows empirical data for two physical parameters: 1) the ultimate bending strength of bone, represented by the solid horizontal line (modified from Biewener 1982; same plot as my Fig. 9), and 2) the cross-sectional area of the humerus and femur midshafts in 27 mammal species (data from Biewener 1983b), which I have divided by body mass to show how their relative cross-sectional area (and strength) decreases with body size. Data for the tibia, radius, and ulna are not shown because they frequently are part of a two-bone system, i.e., the combined support of the ulna-radius and tibia-fibula would need to be considered.

The phenomenon I want to emphasize in Fig. 10 is that the lines for bone strength and mass-specific cross-sectional area (averaged for both bones) cross at nearly the exact same body mass at which MRS begins to decline— around 119 kg. This pattern probably is not just an epiphenomenal artefact, since these three parameters are functionally so tightly linked. Indeed, in the simplest sense body support in mammals is a factor of the inherent strength of boney material and the fact that the cross-sectional surface area of bone decreases relative to mass increases (two thirds rule). I have been discussing at length why this limits MRS and other facets of locomotion, but what I am proposing in Fig. 10 is a precise, functional relationship that predicts 119 kg as the natural limit to MRS, based on the physical properties of boney material and the geometry of vertebrates. This relationship supports the conclusion that speed in small mammals is limited by their absolute size and limited power output, not the strength of their bones. In progressively larger mammals speed increases in conjunction with their ability to generate absolutely more power. At the same time, relative bone strength decreases with size until the crossing point in Fig. 10 is reached, where skeletal safety margins can no longer be maintained without reducing speeds.

Garland's polynomial equation relating top speed to body mass could be used theoretically to predict MRS in an unfamiliar or extinct mammal, such as *Arctodus*. However, while this equation

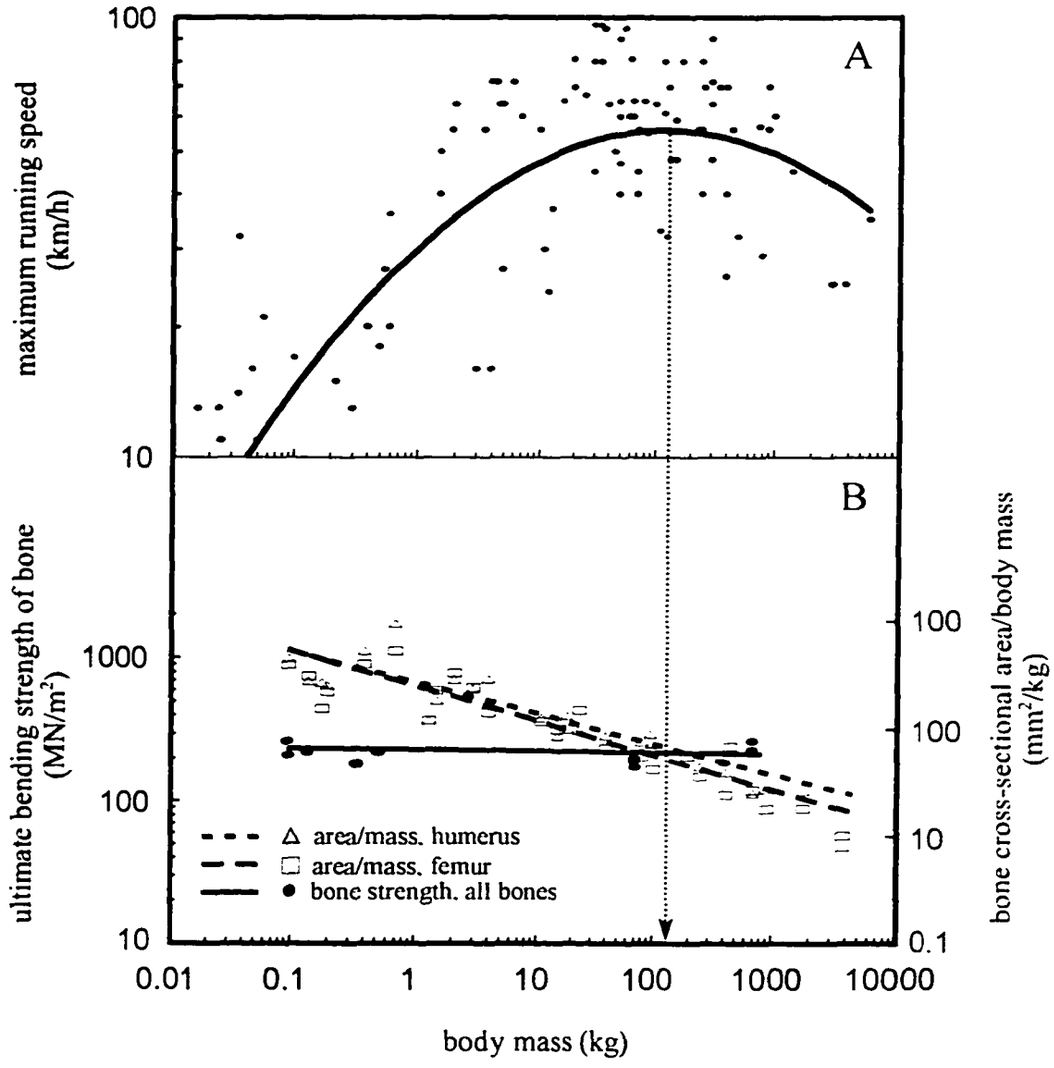

FIGURE 10. The relationship between body mass and maximum running speed (MRS). *A*: Garland's (1983) data for MRS and body mass in a wide variety of mammals. The second order polynomial which best predicts MRS as a function of mass is:

$$\log MRS = 1.47832 + 0.25892 (\log M) - 0.06237 (\log M)^2$$

This function shows how MRS increases with speed until around 119 kg, after which it declines again. *B*: Plots of bone's material strength (solid line) and the relative cross-sectional area of limb bones in mammals (dashed lines; only humerus and femur plotted). The solid line has a slope of zero because the properties and strength of bone do not change with body size. However, the realized strength of a long bone is a function of its cross-sectional area and this decreases (relatively) with size. These two lines intersect around 119 kg, and I am proposing that this relationship between bone property and scaling realities in mammals is functionally significant and ultimately explains why MRS also declines at 119 kg.

accurately describes the *general* relationship between speed and body mass, it does not predict MRS very precisely for any given species, as evidenced by the broad scatter in the data in Fig. 10a. Deviations from the trend line are considerable and reflect morphological adaptations for divergent locomotor and ecological strategies. For instance, cheetahs are around 55 kg, but not all 55 kg mammals would gain selective advantage if they too could sprint at 100 km/h. As with most exercises where an equation is fitted to empirical data, one often gains the most insight about a species by examining the way it diverges from the average trend.

Along similar lines, consider the comparison between goats and large breeds of dogs: both are about the same size (≈ 25 kg), but their skeletal builds are quite different. Dogs run at much higher MRS and engage in higher force activities, and their more massive limb bones reflect this. Biewener and Taylor (1986) showed that these two mammals experience similar peak strains in their bones at physiologically equivalent speeds, including top speeds, but dogs do not reach critical levels of strains until higher speeds because their bones are larger (stronger). Using arguments summarized throughout this chapter, one also may conclude that dogs will fatigue more quickly and use energy at a faster rate than goats running at identical speeds. There is an important conclusion to be drawn from this pattern in pertaining to animals built like *Arctodus*: *coursers built both to run at high top speeds and to maneuver have heavier limbs than similar sized coursers which are adapted for straight-line running or for endurance. Furthermore, as body size increases coursers in the former category must make even greater skeletal compensations because the forces of locomotion increases disproportionately with size*. On the other hand, coursers with lighter limbs typically are adapted for straight line running (often at high speeds), and/or increased endurance; this is especially true in larger mammals.

Other equations besides Garland's have been developed for calculating speeds in animals—either maximum speeds or speeds at gait transitions (e.g., Bakker 1975, Heglund *et al.* 1974, Thulborn 1982) — but these mostly tend to be reliable only over a narrow range of body sizes and shapes. They are especially inaccurate when applied to very large or unusually shaped animals. Furthermore, even though Garland has produced a fairly accurate, if not precise, equation predicting MRS, I believe it is dubious to rely strictly on body mass to predict speed, especially in an animal like *Arctodus* that has an unusual morphology. Alexander and Jayes (1983) have developed a technique for estimating speeds using principles of dynamic similarity and Froude numbers, which are non-dimensional constants that scale quantities of motion to linear dimensions in dynamic systems. Alexander and Jayes' technique is valuable in that it uses readily measurable linear dimensions like leg length or stride length instead of body mass, which can be difficult to estimate accurately. But even this has its pitfalls, as two animals with similar leg lengths do not always locomote in similar ways or at similar speeds. In the next chapter, I will specifically address and estimate speed capabilities in *Arctodus* with an approach that combines both Garland's

polynomial function based on body mass and Alexander and Jayes' technique based on scaled linear dimensions.

Summarizing the Relationships Between Force Generation, Bone Stress, and Body Size

At this point I want to briefly summarize how limitations to locomotion differ in small versus large animals both in terms of their ability to handle dynamic stresses and the ability of their muscles to generate forces. At the beginning of this section I discussed how dimensional analyses predict that smaller animals should have stronger limb bones and experience less bone stress than larger animals. Then I presented evidence which showed that realized stresses in bone do not vary much between animals of different size because large and small animals run in different ways and have different limb architectures. That is, small animals are able to move in ways that, if scaled up, would break bones in larger animals—squirrels can safely jump out of a tree ten times their own height, whereas a large bear or elephant could not. To reiterate, this is because the force of the fall is proportional to the weight of the animal, which increases faster with body size than the strength of its bones.

Relative to their body size, the muscles of smaller animals are proportionately stronger too; they generate relatively more force and work than larger animals (even though their muscles are not relatively much larger). But this is not primarily why a squirrel can leap up to a height many times its own height, whereas a bear cannot. The main reason for this is twofold. First, if large animals jumped that high, they could not take the impact of landing, so they do not engage in that behavior. But more important, very small animals are able to take advantage of their ability to use sharp joint angles and bent limb postures to increase their locomotive power output. They can do this, because the bones of small animals can handle higher bending forces. I showed that muscles which have more time to contract can generate more power and can reach top velocities more quickly, and a crouched stance, often used by smaller mammals, has the effect of increasing the time course of force application because the greater angle of rotation at the joints increases the effective limb length. As Biewener (1983b) points out, this is why a human can jump higher if he/she starts out in a crouched stance. Large animals with straighter legs (necessary so that bending stresses are reduced) have shorter angles of flexion over which their muscles must develop forces of locomotion. To reiterate, this does not mean they generate less force (that is a function of cross-sectional area), but rather less power (the time course of force application). The result is that smaller animals generate relatively more power, and it is primarily for this reason that they are better leapers and accelerators. This also is why small animals can reach top speeds often on the first or second stride, whereas large animals need numerous strides in order to accelerate to top speeds. However, large animals with their longer legs can often reach higher top speeds, and more important, they are able to sustain any given speed for a longer period and over a greater distance.

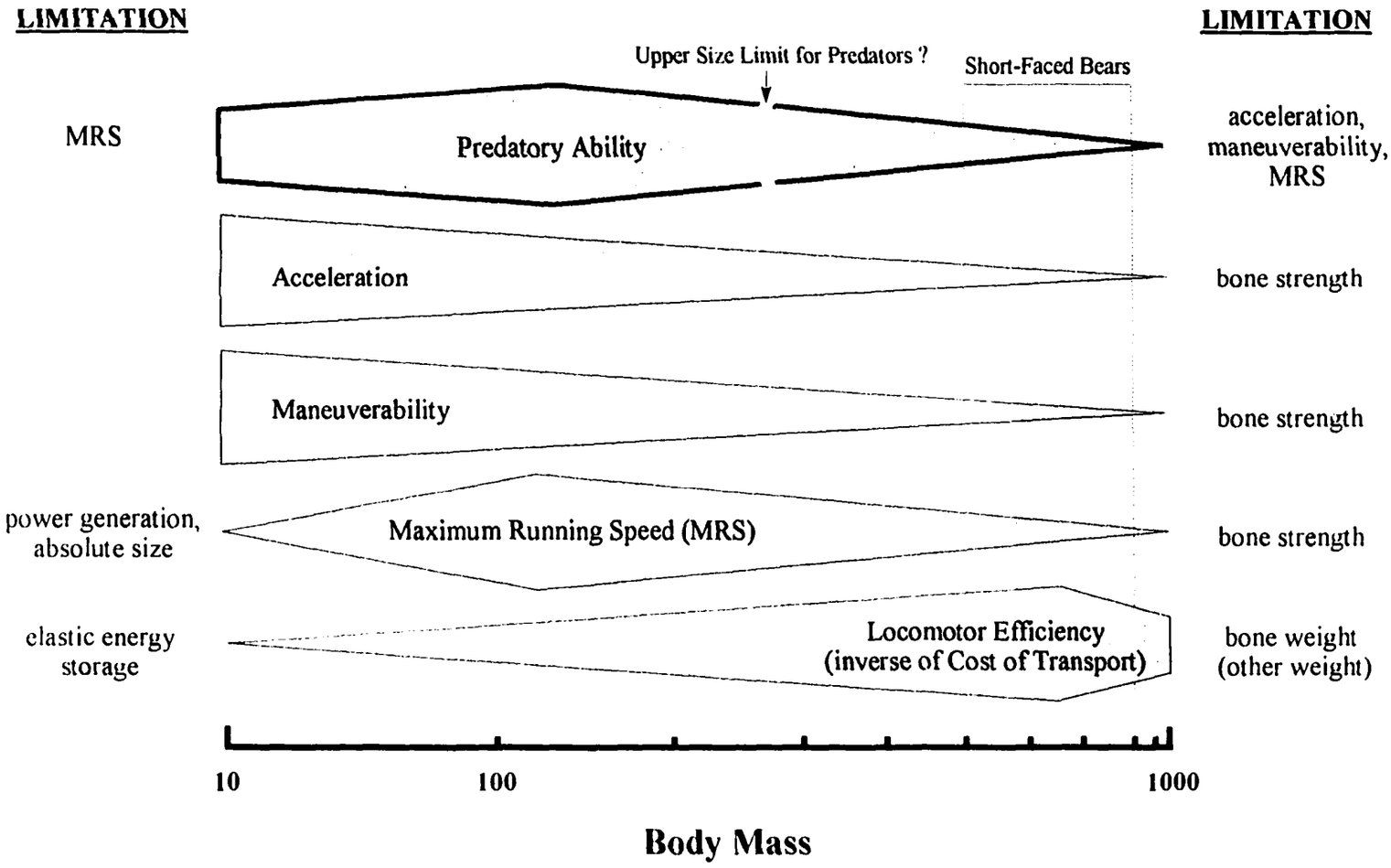

FIGURE 11. Spectrum of locomotor skills in mammals as they relate to body mass. See discussion in text.

So, large and small animals have inherently disparate capabilities and thus exploit different regions of the locomotor spectrum (Fig. 11). Of course, this spectrum is complex and multidimensional, as continuous variables such size and morphology interact with the diversity of locomotor needs of animals. It also is a gradational scale— animals are not accelerators or non-accelerators *per se*, rather there is a continuum between the best and worst accelerators. However, it is realistic to draw certain lines on such a spectrum on one side of which, for example, one would not find a mammal with good enough acceleration, maneuverability, or top speeds to be a viable predator. As I have indicated, the largest terrestrial carnivores that are strict predators today (tigers and very large male lions) rarely exceed 250 kg.

Indeed, bears in general seem to be over the line demarcating reliance on strict predation (although they have builds that also are not made for predation and there are reasons that go beyond locomotor arguments). No brown bears today rely solely on carnivory, much less predation. Polar bears are strictly carnivorous and can reach almost 700 kg, but their form of predation is extemely specialized as it primarily involves waiting to ambush seals at breathing holes and liars. Polar bears also are adept scavengers. Therefore, in order to make the argument that short-faced bears were predatory, one would have to identify a very specific and specialized niche which it exploited. As I follow up on this argument in the next chapter, I will emphasize that this is a tenuous argument that would require strong evidence to support it. Such evidence does not exist. My argument, therefore, will be that short-faced bears, based on their size and build, resided on the locomotor spectrum beyond the line demarcating conventional predatory skills. I think this conclusion has not been reached before because short-faced bears have been perceived as just a sort of super-huge, lean brown bear. Even if this were a morphologically correct statement, the arguments presented thus far show how it would not follow that such a scaled-up bear would experience scaled-up performance.

9. Limbs as Levers

Lever Systems

Machines convert energy into mechanical work. As such, limb muscles are biological machines that use metabolic energy (and stored elastic energy) to generate forces that move the limbs. A limb element rotating around a joint transmits forces from one end to the other and thus constitutes a machine whose mechanics can be described in terms of a lever system and its constituent parts (Fig. 12a). A *fulcrum* is the pivot point of a lever about which turning forces, or *torques*, are generated. Simple levers have two *moment-arms* or lever-arms— an *in-lever* (L_{in}) and an *out-lever* (L_{out}) — which represent the lengths ("arms") of the lever on either side of the fulcrum. *Mechanical advantage* equals the ratio of the two lever-arms ($L_{in} : L_{out}$). Forces are imparted to the in-lever (F_{in}) and generated on the out-lever (F_{out}).

For purposes of this discussion, levers have two turning forces or torques, referred to as *moments*. The *moment-in* (τ_{in}) is equivalent to the force imparted at a point along the in-lever times the length of that point down the in-lever. The *moment-out* (τ_{out}) equals the force generated at a point along the out-lever times the length of that point down the out-lever:

$$\tau_{in} = F_{in} \cdot L_{in} \quad (7)$$

$$\tau_{out} = F_{out} \cdot L_{out} \quad (8)$$

and when $$\tau_{out} = \tau_{in} \quad (9)$$

then $$F_{out} \cdot L_{out} = F_{in} \cdot L_{in} \quad (10)$$

When describing or analyzing a bone-muscle system as a lever system, one frequently is interested in assessing the effect of changing an input value in Equation 10, such as the effect of changing the amount of force applied by a muscle (F_{in}) or changing the length of a lever arm (L_{in} or L_{out}). For instance, the influence of these three values on outforce generation can be stated as:

$$F_{out} = F_{in} \cdot L_{in} \quad L_{out} \quad (11)$$

It is important to note that in addition to generating torques, moment-arms also have characteristic turning velocities, which respond to their lengths in the opposite way as forces. For example,

$$V_{out} = V_{in} \cdot L_{out} \quad L_{in} \quad (12)$$

Limbs essentially move as biomechanical levers. Consider the example of a forearm rotating at the elbow in a running or digging bear (Fig 12b). The fulcrum is at the semilunar notch, the olecranon process acts as the in-lever, and the ulna shaft distal to the semilunar notch acts as the out-lever. When the propodium is extended, such as during the propulsive phase of a stride, the torque delivered to the distal phalanges equals the force of the extensor muscles (long arm of the triceps illustrated in Fig. 12b) times the length of the olecranon process (L_{in}) divided by the combined length of the ulna shaft and hand (L_{out}). In this example, the ulna acts as a first order lever, and Fig. 12 contrasts it to second and third order levers, which also are important in biomechanical lever systems.

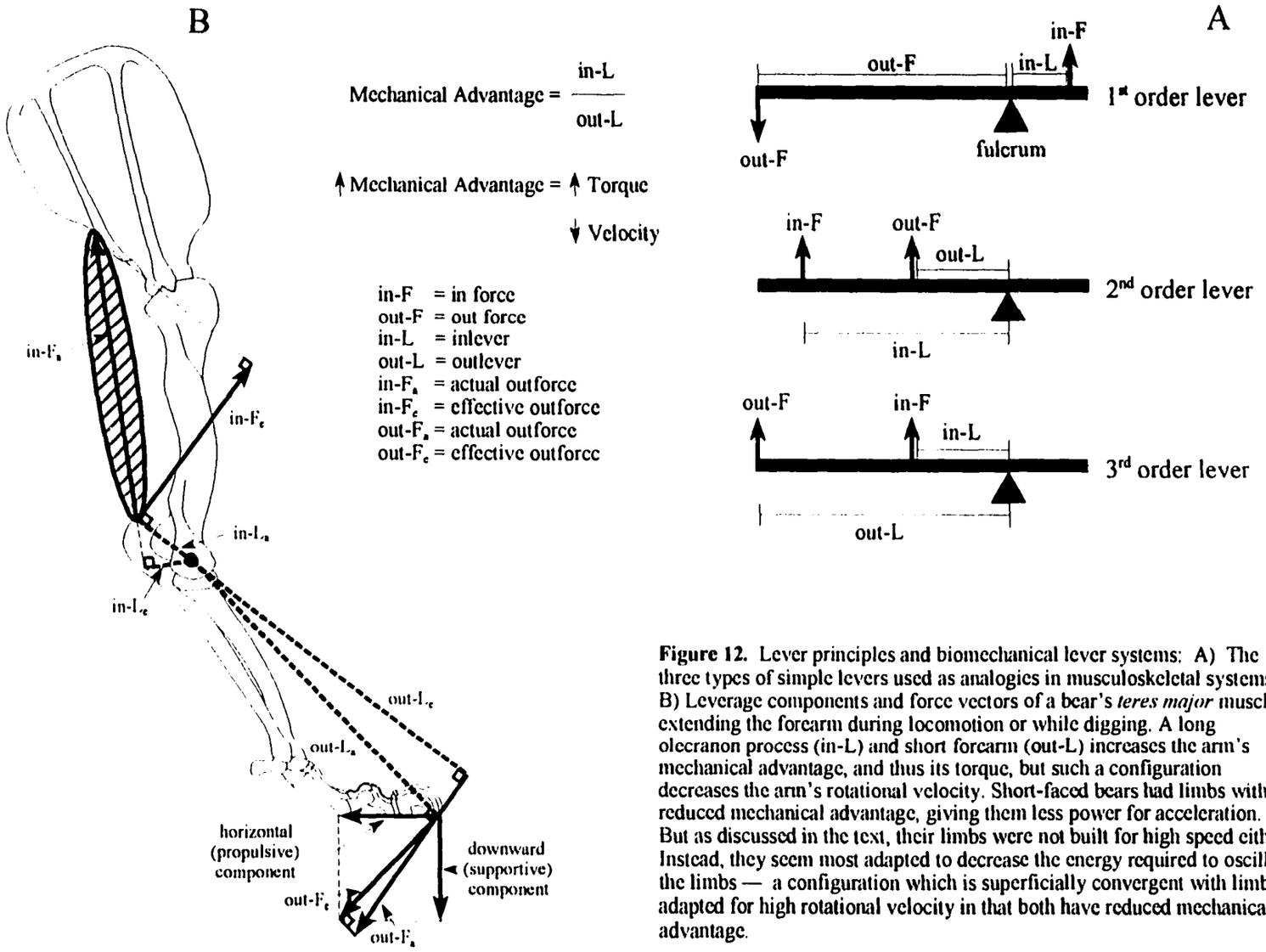

Figure 12. Lever principles and biomechanical lever systems: A) The three types of simple levers used as analogies in musculoskeletal systems. B) Leverage components and force vectors of a bear's *teres major* muscle extending the forearm during locomotion or while digging. A long olecranon process (in-L) and short forearm (out-L) increases the arm's mechanical advantage, and thus its torque, but such a configuration decreases the arm's rotational velocity. Short-faced bears had limbs with reduced mechanical advantage, giving them less power for acceleration. But as discussed in the text, their limbs were not built for high speed either. Instead, they seem most adapted to decrease the energy required to oscillate the limbs — a configuration which is superficially convergent with limbs adapted for high rotational velocity in that both have reduced mechanical advantage.

The Effects of Mechanical Advantage on Locomotor Performance

In the next chapter, I will show that the olecranon process and a number of other inlevers of short-faced bear limbs were shortened compared to other bears, reducing their mechanical advantage. The remainder of this discussion considers the functional ramifications of lever lengths and mechanical advantage on locomotor performance.

Compare the mechanical advantage and muscle configuration in a limb built for high rotational velocity versus one built for high torque or high power (at this point it is not appropriate to compare energetic efficiency or economy of effort). From Equation 12 it is apparent that rotational velocity is increased by a long outlever, short in-lever (high L_{out}:L_{in}), and by fast contracting muscles. Recall that fast contracting muscles generate less force and they use energy more quickly. Also, speed of contraction is inversely proportional to muscle length, so fast muscles tend to be short. If they also are not large, they will perform less work because work ∝ volume. So, limbs modified for increased rotational velocity will sacrifice strength and will fatigue quickly, although I have shown that running specialists make other modifications to increase endurance.

A limb designed for high torque will have increased mechanical advantage (low L_{out}:L_{in}) and muscles that generate high forces and perform greater work. I showed that muscles with these traits typically are large and contract slowly. If the limb also is to be moved with high power output (recall power equals the rate that work is done or the velocity of force application), then the muscles also must contract rapidly. In doing so, they fatigue quickly. Therefore, one can distinguish between a limb built strictly for high torque versus one built for power. The muscles of the high torque limb will contract slowly and fatigue slowly. This is what one finds, for example, in fossorial mammals that must dig continuously but not rapidly (Hildebrand 1985c), or as I showed earlier, in turtles which move a lot of weight, but slowly. The muscles of a high power limb, on the other hand, generate forces at a high velocity, such as when a brown bear excavates a ground squirrel hole or when a lion accelerates after prey. Both high power and high torque limbs will have relatively high mechanical advantage.

What are the performance ramifications of limbs that evolve for high rotational velocity, versus limbs that evolve for high torque or high power? In the case of the fossorial mammal, I showed that high-torque limbs perform a lot of work, but slowly. These animals conduct strenuous locomotor activities for long periods, but not quickly. Limbs that evolve to rotate at high velocity are obviously adaptive for high speed locomotion, however, *a strictly fast rotating limb is not optimally designed for acceleration because acceleration requires power to get the limbs up to speeds quickly*. Therein lies the need for powerful limbs in accelerators. While both fast and powerful limbs may reach the same ultimate velocity, animals with powerful limbs will get up to speeds more quickly, while animals with "fast" (but not powerful) limbs will fatigue less quickly, and thus will be able to run longer and farther.

Runners evolve morphologies that balance their needs for power, speed, and endurance. But if one thinks of limbs only as simple levers then an obvious paradox arises: why don't "fast-limbed" animals also increase power and acceleration by increasing muscular input? This question arises because my comparison of limbs, so far, has assumed that all limbs are identical, except for their mechanical advantage and muscle input. This assumption is wrong. It ignores the fact that limbs have mass and the fact that changes to parameters such as L_{in}, L_{out}, and muscle volume impact the quantity and distribution of limb mass. This mass costs energy to move, and this cost varies based on the muscle's position on the limb and its rate of acceleration. These are matters of kinematics and are discussed in the next section. After that discussion, I will bring together all of the previous issues and present an overview of locomotor adaptations for speed, acceleration, and endurance.

Low Gear and High Gear Muscle Systems

Before moving on to kinematics, I want to briefly discuss "low gear" and "high gear" muscles, since this concept relates principally to lever dynamics and mechanical advantage. In a classic paper, Smith and Savage (1956) elaborated on the ways that muscle configuration and the placement of muscles on a limb will enhance either the speed or power of their action. Hildebrand (1995) calls these high gear and low gear muscles, respectively, as the former are used for maintaining high speeds with the least effort and the latter are used for acceleration.

Figure 13 (modified from Smith and Savage 1956) shows a hind limb of a bear illustrating this concept. The gluteal group and the femoral group are the two main muscle groups that extend the femur about the acetabulum[7]. A perpendicular line (L_{in}) drawn from the acetabulum to each muscle's line of action represents its inlever length. A vertical line (L_{out}) from the acetabulum to the ground represents the system's outlever length (the same for both muscles). The ratio L_{in}:L_{out} is clearly different for these two muscle groups when the femur is in the position shown (note that each muscles' mechanical advantage changes with the angle of flexion). Assuming that the length of contraction in a given unit of time is equal for each muscle, then the gluteal group will swing the femur through a greater arc than the femoral group during that period of contraction. However, the femoral group imparts more force because of its greater mechanical advantage.

From this example, it can be seen how the gluteal muscles are considered to be high gear muscles that maintain steady state locomotion at a minimal cost, whereas the muscles on the posterior surface of

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[7] The gluteal group is comprised of the *g. minimus* and *g. medius* which originate primarily on the dorsal-lateral surface of the ilium (and partially on the lumbar vertebrae) and insert on the greater trochanter of the femur. The femoral group is comprised of the *biceps femoris*, *adductor femoris*, *gracilis*, *semitendinosus*, and the *semimembranosus*, which originate on the posterior and dorsal surfaces of the ischium and insert at various points along the posterior edge of the femur and the proximal tibia.

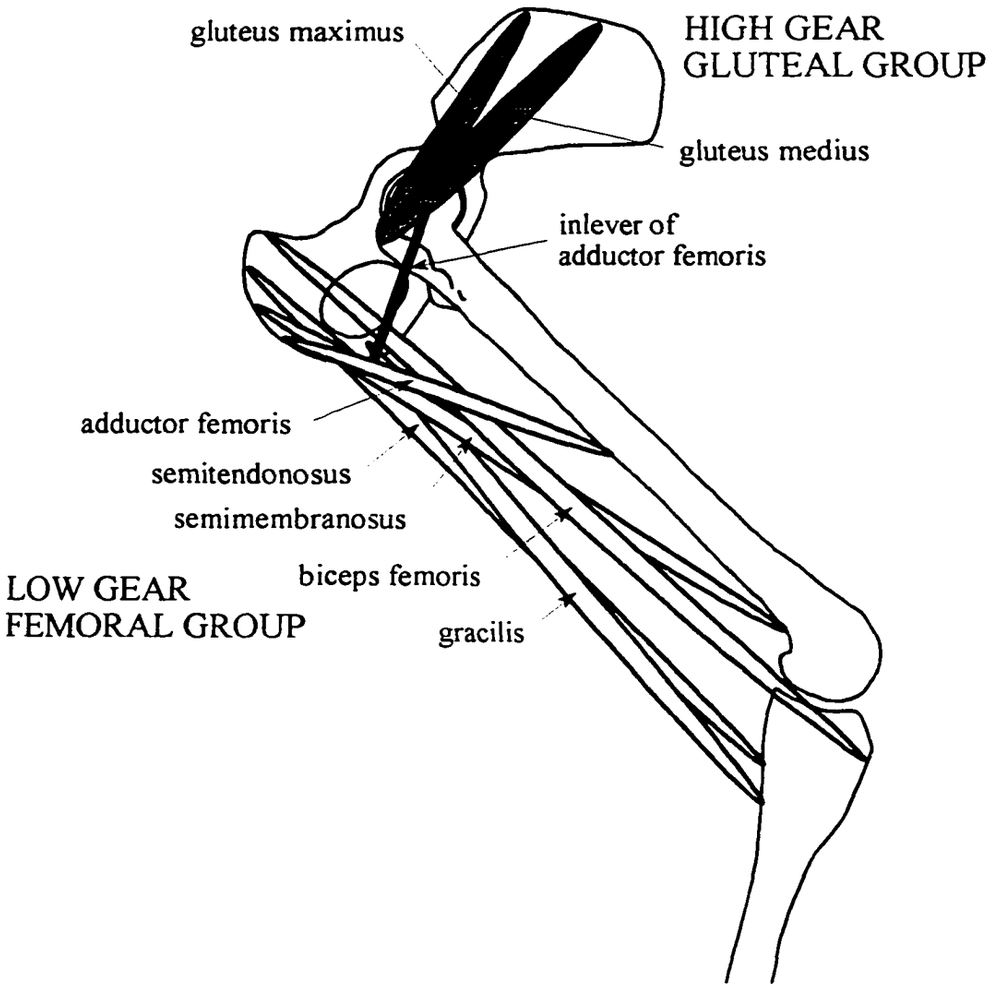


FIGURE 13. High and low gear muscle groups used by a bear to extend its femur. "Gearing" relates to the relative length of each muscle's inlever (moment arm), drawn as a perpendicular line from the acetabulum to the muscle (inlever shown for adductor femoris only). Short inlevers, such as those for the gluteal group, have reduced mechanical advantage, so they provide little power. However, they require very little energy to extend the femur at high speeds compared to low gear muscles. Thus, they are used mainly to sustain steady state speeds. The femoral muscles have long inlevers (greater mechanical advantage) and provide power for acceleration. They are less efficient than the gluteal muscles and fatigue more quickly. Position of insertion points and leg length also affect mechanical advantage. For example, configuring femoral muscles with more proximal insertion points will reduce their mechanical advantage and thus will decrease power output, but increase efficiency, meaning they will fatigue less quickly. Long legs have a similar effect because they increase outlever lengths, and their longer muscles fatique less quickly. Short-faced bears had longer limbs and more insertion points compared to other bears, which increased their locomotor efficiency but reduced their ability to accelerate. (Concept for drawing adapted from Smith and Savage 1956.)

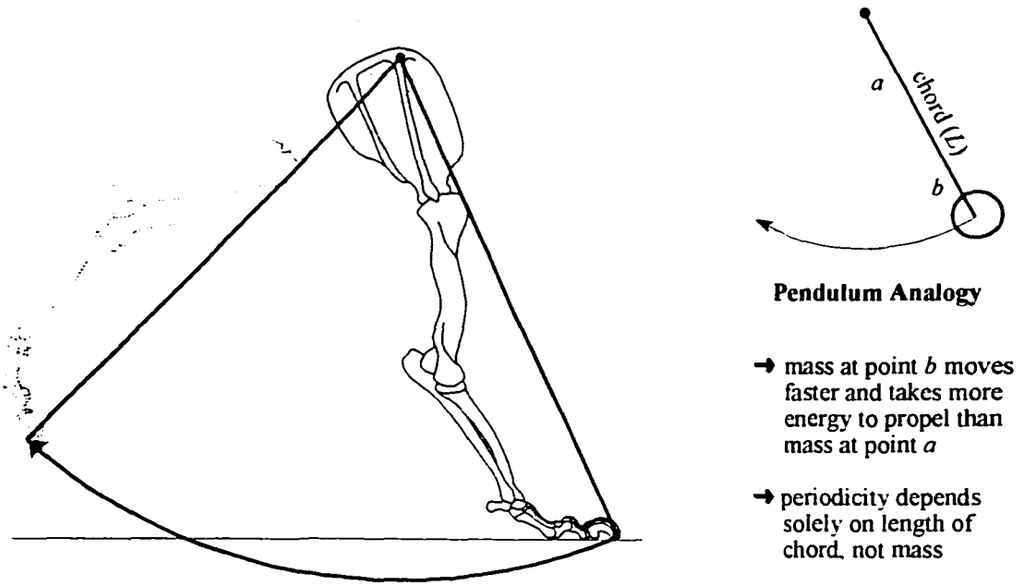
the hind limb provide most of the power and acceleration for locomotion (and other activities). When it comes to fossils, one cannot always identify the precise attachment points of individual muscles on bones, but often it is possible make some qualitative assessments about the relative importance of high gear and low gear muscles by analyzing dimensions of limb bones (such as the femur) and girdles (such as the pelvis). In the next chapter, I will make these assessments on *Arctodus* and show that it primarily had evolved a musculoskeletal configuration of the high-gear sort.

10. Kinematics of Limbs

So far, I have considered the whole body metabolic costs of locomotion, the effects of scaling on musculoskeletal performance, and the configuration of limb levers. For the most part, these were discussions about factors limiting energetic *input* in animals. Next I want to consider the *output* side of the equation— the amount of energy required to move a given mass. This is something paleobiologists can assess more easily on a fossil, even if just in relative or qualitative terms.

Physiologists assert that most of the energy spent on locomotion is used to elevate the body's mass, and that only a small percentage goes to limb oscillation. Yet anatomists have always emphasized the energetics of swinging the limbs and kinematics as central themes in interpreting limb morphology. *Kinematics* addresses the mechanics of objects (masses) in motion (*dynamics* address the *forces* associated with motion), and as stated in the previous section, any consideration of design principles and performance features in limbs is incomplete without accounting for the quantity and position of the mass being moved.

If one thinks of limbs as oscillating masses swinging back and forth during the course of a stride sequence (Fig. 14), it can be seen that each limb passes through four energetic phases relative to the rest of the body (two acceleration phases and two deceleration phases): 1) when the limb is swung forward, energy is expended to overcome inertia and for acceleration, 2) at the end of its forward motion, energy is expended to decelerate the limb's momentum to zero, 3) next, energy is expended to overcome the limb's resting inertia and accelerate it rearward, 4) to end the cycle, energy is expended to decelerate the limb's rearward motion, setting it up for phase 1 again (Hill 1950; Alexander *et al.* 1979; Fedak *et al.* 1982; Hildebrand 1985a, 1995). Certain mechanical aspects of these four phases can be described using principles of oscillating masses and pendulums, with a few qualifications (Fig. 14). First, the energy expended during each phase is unequal (Manter 1938, Fedak *et al.* 1982). Also, the rearward acceleration phase must lift and propel the animal's body mass, which requires more energy than the forward (recovery) phase. Energy expended for the two deceleration phases are unequal, too, since contact with the ground on the forward phase helps brake the limb's momentum



Force of Acceleration $\tau = I \cdot \alpha$ ($F = m \cdot a$)

where I is moment of inertia $I = m \cdot D$ and D is the distance from the pendulum's pivot point to its center of mass (equivalent to L in a simple pendulum)

Energy of Oscillation $E = \frac{1}{2} I \cdot \omega^2$ ($E = \frac{1}{2} m \cdot v^2$)

Periodicity $T = 2\pi\sqrt{L \cdot g}$

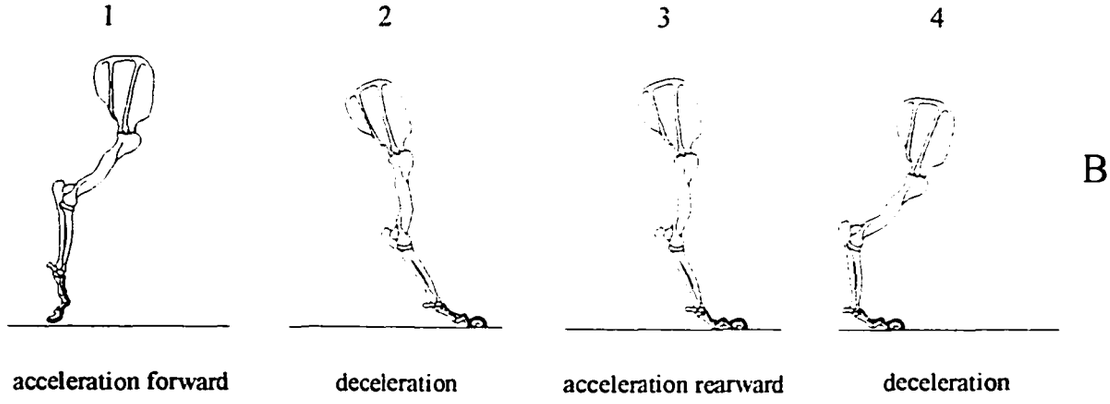


FIGURE 14. Kinematics of oscillation in the front limb of a bear. A) An oscillating pendulum provides a useful analogy for understanding kinematic ramifications of mass distribution and leg length in terms of energy costs associated with acceleration and maintaining limb velocities. B) The four energetic phases of oscillation in a limb — *see text for discussion.* (Curvilinear and rectilinear formulae shown, with the latter in parentheses)

The energetic cost of each oscillation phase is dependent on two factors: the limb's inertia, which is directly proportional to its mass, and the limb's momentum, which is proportional to its mass times velocity. It takes more energy to move and stop a greater mass, but in terms of energy expenditures, the distribution of mass along the limb can be more important than total mass. Distal mass is more expensive to move than proximal mass for the following reasons. Consider a limb traveling through an arc, similar to a swinging pendulum (Fig. 14). Distal masses on the limb oscillate at higher velocities than proximal masses, and the energy required to move a given mass increases as the square of its velocity:

$$E = {}^1\!/_2\, m \cdot v^2 \tag{13}$$

where E is the kinetic energy of motion, m is mass, and v is velocity. The motion of limbs usually is more accurately quantified by curvilinear equations, but rectilinear equations are more intuitive so I usually will refer to both. The rectilinear equivalent of Equation 13 is:

$$E = {}^1\!/_2\, I \cdot \omega^2 \tag{14}$$

Where I is the momentum of inertia, and ω is angular velocity.

The energetic relationship between mass and velocity explains why distal masses, which travel at greater velocities, are more expensive to propel in an oscillating system. However, it is perhaps more germane for this discussion to think in terms of the force required to accelerate a limb, and the effect of mass on acceleration, as opposed to simple velocity. Here, I draw from Newton's Second Law:

$$F = m \cdot a \tag{15}$$

where F is force and a is acceleration. Its curvilinear equivalent is:

$$\tau = I \cdot \alpha \tag{16}$$

where τ is turning force (torque) and α is angular acceleration. The moment of inertia (I), is a measure of an object's resistance to acceleration/deceleration and, in a curvilinear system, equates to mass times the square of the radius of gyration (D):

$$I = m \cdot D^2 \tag{17}$$

Conceptually, D is the distance from a pendulum's pivot point (e.g., hip, shoulder) to its center of oscillation, which is essentially the limb's center of mass (Hildebrand 1985a). If legs were simple pendulums, which assume that a concentrated mass is suspended from a weightless chord, then the length of the limb would suffice for D. Since legs are unevenly shaped and have masses that vary along their lengths, D is difficult to measure but can be assessed qualitatively. From Equations 15 and 16 it is apparent that limbs which are heavy distally are disproportionately costly to accelerate/decelerate because their moment of inertia increases by mass times the square of that mass's distance down the limb (Equation 17).

Given that $a = v \cdot t$, Equation 15 can be rewritten as:

$$F = m \cdot v \cdot t \tag{18}$$

This relationship between mass, velocity, and time of force application has critical implications for the evolution of limbs. First, it means that heavy limbs, especially those that are heavy distally, require forces to be applied for a longer period in order for the limb to reach a given velocity. It other words, it will take a distally heavy limb more time to reach a maximum velocity for a given level of force application compared to a limb of similar mass but with its weight more proximally distributed. Equation 18 also dictates that a long limb will take more time to reach a given velocity than a short limb (for the same force application) because its distal segments must be accelerated to greater velocities (as per the pendulum discussion above). This equates directly to poorer acceleration, unless more force can be applied, which is a principle reason why long legs are generally counterproductive for acceleration. However, Equation 18 dictates that long-legged animals potentially can achieve higher overall velocities because they have a longer period of force application (i.e., longer strides), even though it will take them more time to reach those velocities.

Looking at these relationships from the opposite point of view, Equation 18 also dictates that *less force is required to swing a limb at given velocity if more time is available to apply that force*. That is just what long legged animals accomplish through longer strides. Long-legged animals take longer strides because, like a pendulum, their limbs swing with an inherent periodicity (T, the time taken to complete an oscillation) that is based solely on their length (L):

$$T = 2\Pi \sqrt{(L/g)} \tag{19}$$

where g is the constant of gravity (Hildebrand 1985a). Note that mass plays no role in determining this

rate, and that longer legs will have a longer natural periodicity. The principle of natural periodicity in oscillating limbs explains why long-legged animals will have inherently slower stride rates compared to short-legged animals traveling at similar speeds, and if fewer but larger strides are taken to cover a given distance at a given velocity, then the animal expends less energy. This deduction agrees with the pattern found by physiologists described in earlier sections (e.g., Kram and Taylor's (1990) results). Recall too that longer muscles contract more slowly, and in doing so generate greater overall forces and use energy more efficiently.

It is a common axiom that coursers increase the lengths of their distal limb segments over the course of their evolution, and that many coursers (including fast runners) have long legs. This is not contradictory to the kinematic arguments presented here because coursers evolve limbs that are light distally so that increasing limb length does not add significant distal mass or inertia to the limb compared to the advantages gained by increasing stride length. The result is increased efficiency and often increased top speed (if the animal is not very large).

So although long-legged animals need to oscillate limbs that by definition have longer distal portions, they can do so more efficiently and without bulky muscles as long as acceleration is sacrificed. Their long strides mean that a given distance can be covered more efficiently because the time of force application can be long and slow, and thus less total force needs to be applied. And I showed how, from a kinematic standpoint, long-legged animals do not necessarily need to sacrifice speed, either. Garland's (1983) data on top speeds in mammals, however, seem to indicate that there is a limit to this strategy, which I argued is determined by limits to bone strength— once a leg gets very long or body mass gets very high, bending moments become too great, especially from the forces generated at high speeds and during rapid acceleration. This effect begins to limit speed, and especially acceleration, in animals that get much over 150 kg (Garland's value is 119 kg, but it is an averaged value and I think the real weight limit is probably somewhat higher). Another way to look at this phenomenon is that increasing leg length helps increase top speeds— *to a point*. That point is reached if legs get too long, or if the mass supported by the limbs becomes too great. Of course, in most cases, both factors come into play but to differing degrees depending on an animal's individual morphology.

In the previous section on levers, I poised the following question: why could not an animal built for sustained running at high speeds also be built for increased power, thereby also making it a good accelerator? For example, why haven't ungulates done this in order to both out-accelerate and out-distance a predator? By now the answer should be apparent: by adding the muscles needed for increased power, animals add weight and hence decrease endurance. Also, powerful animals increase the mechanical advantage of their limbs and this, too, decreases endurance and potentially decreases limb velocity. Plus, an animal that has evolved powerful muscles with high mechanical advantage in addition to long, light

limbs would most likely break those limbs if it tried to run fast, accelerate rapidly, or make any sharp turns. If in response to this dilemma the limb bones are made stronger, they would be more expensive (kinematically) to swing and this hypothetical ungulate would look more like a carnivore, not an ungulate. It would neither be able to out-distance a predator, nor would it be as efficient at foraging as its competitors.

11. Summary of Relationships Between Morphology and Locomotor Performance

Throughout this discussion I have been explaining the effects of specific morphological traits on performance aspects of locomotion, such as top speed, acceleration, or endurance. In this summary section, I want to turn the question around and describe the morphological patterns one would predict to find in a large courser built either for acceleration, high top speed, or endurance. I will show that there is much overlap in the latter two categories, but that good accelerators stand out because of their powerful builds, high mechanical advantage, and minimal regard for improving kinematics.

Good Accelerators

Earlier, I said that good accelerators should have muscles which generate high forces, but which are not too heavily loaded, so they can also contract quickly (recall that speed of contraction is a primary determinant of power). One key to this formula is leg length. Short limbs normally will have shorter outlevers (low L_{out}:L_{in}), increasing mechanical advantage and thus power. Shorter legs also have shorter muscles, which inherently contract more quickly; as long as these muscles have large volume, this becomes a formula for generating high power. Kinematically, short legs have less distal mass, which makes them less costly to accelerate. But short legs necessitate increasing stride rate to achieve a given speed (since stride length is reduced), and this is energetically costly. But I also showed that animals with long legs and long stride rates take longer to reach top speeds, and that short legs taking rapid strides are able to reach these velocities quicker. Therefore, one would expect the best accelerators to have short legs with short, massive muscles.

Good accelerators sacrifice traits which would make them more efficient for the sake of increasing power output. In order for their bones to be stronger, they are necessarily heavier. Moreover, configuring muscles for high mechanical advantage decreases their turning velocities. To make up for this and still achieve high speeds, good accelerators have short legs thereby eliminating distal mass. This is equivalent to running a car at very high speeds in a low gear, or with very small tires. Such a car, or animal, accelerates well, but is very inefficient and its top speed is limited.

Efficient Runners

Coursers that have evolved to run efficiently and reduce the cost of transport share a host of diagnostic traits that contrast sharply with those found in good accelerators. Universally, efficient coursers reduce overall body weight, which decreases the energy expended lifting the body's mass during each stride. Efficient coursers also evolve legs that are light and long. Long legs increase stride length, reducing the rate of force application and giving the legs more time to reach a given velocity during each stride. This reduces the cost of transport because the muscles can contract more slowly and thus more efficiently. Light limbs, especially those that are light distally, are important for coursers with long legs because distal mass in an oscillating system is expensive to move, and with long legs there is a larger distal region. However, when high speeds are not the goal, distal mass is less of an issue since its mechanical effect increases disproportionately with speed. Coursers built for efficiency also tend to be larger-bodied because the cost of transport is inversely proportional to body size. This is mainly because larger animals have relatively longer legs, but also because larger animals are more able to store and release elastic strain energy in stretch tendons.

Features that improve acceleration are not common in efficient runners, and in fact, acceleration is directly compromised by long, light limbs and a large body. Long limbs are especially damning to accelerators for at least four reasons: 1) long limbs reduce mechanical advantage, 2) long limbs typically have long, slender muscles which do not generate high power output, 3) in oscillating systems, longer chords (limbs) take longer to reach maximum oscillating velocities because portions that are more distally located ultimately have to be accelerated to a greater velocity, and 4) long limbs generate larger bending moments and greater bending strains in their bones. In addition, light limbs are not strong enough in large mammals to handle the sudden changes in velocity incurred during acceleration, deceleration, and quick turns because dynamic stresses of these high force activities increase disproportionately with size relative to bone strength. So, whereas a good accelerator can leap to top speeds in a couple of strides, often from a crouched stance, efficient runners can not generate enough power for such feats or handle the stresses, so they take more strides to get up to maximum speed. Efficient runners often can reach high speeds, but such coursers do not have the bone strength necessary to handle sharp maneuvers at high speeds, and I showed that very large size limits speed. Indeed, it was shown that maximum running speeds in all mammals are limited by the strain limits of bone, not the ability to generate force or power.

Because small and moderate-sized animals experience relatively less dynamic stress than very large animals during equivalent locomotion, they are better suited to exploit niches that depend on acceleration, speed, and agility. In fact, if an animal has evolved such skills, one would predict selection to favor a modest body size, and perhaps even a reduction in body size if its ancestral stock was large-

bodied. For instance, a bear evolving into a predatory niche would almost certainly evolve a body size smaller than an average bear. On the other hand, very small animals are limited in their ability to generate enough absolute power and speed to be good predators, and there can be some incentive for them to increase body size, depending on the size of their prey.[8] But this logic does not hold for very large mammals for all the reasons discussed in this chapter, and I showed that once a mammal exceeds around 150 kg, it must reduce top speeds and curtail other activities which a smaller animal can perform safely.

Taken together, these axioms of body size mean that most animals could reach greater absolute top speeds and accelerate to them more quickly by increasing body size. But this strategy works only up to a point (up to a certain body size), after which both top speed and acceleration, but especially the latter, decrease (recall Fig. 10). It is these two competing factors that act to constrain body size in predators.

In the next chapter I discuss specific locomotor adaptations in *Arctodus* and discuss why this bear seems to clearly fall in the category of an animal that had evolved to decrease the cost of transport and not for increased speed or accelerating abilities. These facts and others discussed in the fourth chapter on ecological energetics portray a bear which did not evolve as a powerful superpredator, but rather as a lanky, far-roaming bear, which I propose was a unique scavenging specialist on Pleistocene landscapes.

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[8] Because very small predators are relatively limited in performance, they most commonly hunt prey much smaller than themselves. In that case, predators truly are much larger than their prey in order to outperform them

CHAPTER III

THE LOCOMOTOR ADAPTATIONS AND ECOMORPHOLOGY OF SHORT-FACED BEARS

PART II: SPECIFIC MORPHOLOGICAL FEATURES OF *ARCTODUS* [1]

1. INTRODUCTION

In the previous chapter I reviewed general features of locomotor dynamics in large quadrupedal mammals. In particular, I examined the ways that body size and limb configuration relate to an animal's ability to accelerate, maneuver, and run at high speeds, and I discussed how scaling factors limit these activities. I showed how all mammals undertake locomotor activities within uniform and predictable safety margins, but that the dynamic forces of locomotion increase with body size faster than the skeletal system's ability to dissipate these forces. This means that high force activities such as rapid acceleration, rapid maneuvering, and running at high speeds, which are critical for predators, become increasingly stressful in larger animals. Therefore, larger animals curtail such activities, which is the primary reason why modern terrestrial predators do not exceed much over 250 kg.

Accordingly, one can phrase the competing foraging models for *Arctodus* (predatory versus scavenging) in terms of their implicit predictions about this bear's locomotor capabilities and post-cranial morphology. These predictions then can be tested using the principles laid down in the previous chapter and morphometric data from *Arctodus*. This chapter examines and tests these predictions.

Paleontologists have suggested a wide range of potential prey species for *Arctodus*, including proboscidians (*Mammuthus* and *Mammut*), giant ground sloths (*Megalonyx*), giant beaver (*Castoroides*), bison (*Bison*), musk oxen (*Ovibos* and *Bootherium*), horses (*Equus*), camels (*Camelops*), peccaries (*Platygonus* and *Mylohyus*), caribou (*Rangifer*), moose (*Cervalces*), wapiti (*Cervus*), and deer (*Odocoileus*) (Kurtén 1967a; Harington 1977, 1996; Richards and Turnbull 1995). Given the diversity of body sizes and running speeds found in these potential prey, I think it is best to subdivide the predatory model into two sub-hypotheses: those suggesting *Arctodus* had evolved as a fast cursorial predator specializing on faster, moderate-sized prey, and those suggesting *Arctodus* had evolved to overpower larger, but slower, Pleistocene megaherbivores.

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[1] This chapter was written as the second part of a three-part monograph on the locomotor adaptations and ecomorphology of short-faced bears. Chapters 2 and 4 constitute the other two parts.

The first hypothesis predicts *Arctodus* to have had features adaptive for either high acceleration (if it was an ambush predator) or high top speeds (if it was a pursuit predator). In either case, this hypothesis predicts that *Arctodus* should be fairly maneuverable at high speeds. As a cursorial predator then, *Arctodus* should have evolved limb muscles which could generate high power and limb bones which were strong enough to handle the high stresses of these activities. It also follows from the previous chapter that one would expect a predatory bear using either ambush tactics or cursorial pursuit to evolve a relatively smaller body size, because modern bears tend to push the limits of body size and running abilities (data in the previous chapter showed that in order to handle the stresses of these activities it would be necessary for a very fast bear, or one that accelerated rapidly, to evolve a smaller body size).

The second predatory hypothesis— that *Arctodus* had evolved to overpower very large megafauna— carries certain morphological predictions that differ from the cursorial pursuit hypothesis. First, it does predict large body size, because this would be advantageous for capturing and killing very large prey. But for the same reason, this hypothesis predicts that such a predator would evolve a strong robust build so that it could overpower animals the size of proboscidians and ground sloths, for example. Such prey species are not fast, and it would not require much speed, acceleration, or maneuvering at high speeds to catch them, so one would not expect to find many cursorial features, especially limb-lightening, in this type of predator.

Contrasting with these two predatory hypotheses is my proposal that *Arctodus* functioned as a specialized scavenger, a model which also carries a series of morphological predictions. First, based on the assumption that large mammal carcasses would be dispersed far apart and found at unpredictable frequencies (Chapter 4), it predicts selection for increased locomotor efficiency because *Arctodus* would have had to search very large home ranges while foraging. I showed in the previous chapter that locomotor efficiency is gained by increasing body size, reducing relative body weight (i.e., a bigger but more gracile body), and increasing leg length. Thus, these are the main postcranial features predicted by the scavenging model. Since such a scavenger would not need to pursue and catch prey at fast speeds, or accelerate rapidly, it could sacrifice limb strength and power production in exchange for muscular and kinematic efficiency. This model predicts that *Arctodus* would experience additional selective pressure to increase body size because a larger body would make it a better competitor against other carnivores that challenged it for control over carcasses. In the next chapter, I discuss how a larger animal also is better suited metabolically for dealing with an unpredictable boom-and-bust resource such as carrion.

There are two main sections to this chapter. In the first, I address the fundamental question of whether *Arctodus* was cursorially adapted. To do so, I examine the proportions of its limbs both in absolute terms and using allometric analyses whereby I compare *Arctodus* with other bears and other Carnivora. This provides insight into the direction of *Arctodus*' divergence away from it relatives. Then I

evaluate important conformational features of its appendicular and axial skeleton, examining how *Arctodus* swung its limbs for more clues into the cursorialism debate. In the second section, I reconstruct the gait, speed, and locomotor style of short-faced bears by taking a new look at the relationship between *Arctodus*' leg length and back length, and by drawing upon some formulae discussed in the previous chapter. The multitude of morphological evidence presented throughout this chapter most strongly supports the hypothesis that this carnivore was cursorially adapted and optimized for sustainable long range locomotion at moderate speeds— traits which are more adaptive for a scavenging specialist than an active predator. In the next chapter I examine the ecological implications of this niche and propose a model for how it evolved in Pleistocene environments.

2. WAS *ARCTODUS* CURSORIALLY ADAPTED?

To many paleontologists, the degree of cursorial adaptations in *Arctodus*' is the primary unresolved issue preventing us from reconstructing specific aspects of this bear's foraging ecology and life history. In his predatory model, Kurtén (1967a) used relative limb length to argue that *Arctodus* was highly cursorial, and capable of achieving high speeds, but Emslie and Czaplewski (1985) interpreted the data on limb length differently, and argued that *Arctodus* was non-cursorial (discussed below). Even though stable isotope data reveal that *Arctodus* was carnivorous, there still are a number of different ways that *Arctodus* could have locomoted and foraged for meat, as outlined above, meaning the cursorial question is still of prime importance. Indeed, questions about *Arctodus*' predatory skills (i.e., was it a high speed pursuit predator, an ambush predator that relied on rapid acceleration, or a scavenging specialist built for locomotor efficiency) seem mute if one can not first establish whether or not it had cursorial advancements over other bears. Traditionally, this debate has focused on discussions regarding the relative lengths of proximal and distal limb segments. I will review this evidence and explain why proximal-distal limb length is a poor indicator of cursorialism in bears, followed by a look at other indicators that provide better clues into *Arctodus*' cursorial abilities.

Proximal-Distal Limb Proportions

The ratio of proximal:distal segment lengths in limbs is often used as an indicator of cursorialism for kinematic reasons discussed in the previous chapter. To reiterate, as cursors evolve longer legs the distal segments almost always become preferentially elongated because they are lighter. The problem with applying this principle to *Arctodus* is that it does not work very well in bears, which have very heavy distal limb segments due to their large unspecialized feet. It would not be of any kinematic advantage for a

bear to evolve relatively longer distal limb segments without concomitantly making them lighter. This would include reducing the size of the feet and the robustness of the propodia. In fact, elongation of distal limb segments may be a poor indicator of cursorialism in animals that are in the early stages of cursorial evolution, especially in an incipient courser whose ancestors possessed large feet. With these qualifications in mind, I will briefly review the patterns of elongation found in *Arctodus* and other bears.

Humeroradial (R/H) and Femurotibial (T/F) indices for short-faced bears as well as other bears and other Carnivora are shown in Table 4. These indices demonstrate how the distal two bones (radius and tibia) are relatively unmodified in bears, including short-faced bears, compared to traditional cursorial species. Often, R/H and T/H values exceed 90 - 100 in lions, cheetahs, other felids, canids and cursorial ungulates (Gonyea 1976), but they are much lower in bears and the index values for *Arctodus* are not appreciably different than for other ursids. The greatest difference between bears and other more specialized carnivores appears in the proportions of the hind limb. Table 5 shows the relative contribution of each bone (including metapodials) to limb length in a variety of bear species. These values also reveal that the relative composition of the limbs is similar among bears, and that the distal bones of *Arctodus* are even somewhat shortened.

Values for limb segment lengths in the single *Arctodus* specimen measured by Emslie and Czaplewski (1985) are shown in Table 4. This bear had unusually low R/H and T/F index values, which these authors used as evidence against cursorialism. Moreover, they chose to compare this specimen to modern brown bear samples which included some individuals with unusually high indices (values in Table 4). Still, these authors argue that their value for *Arctodus* is more accurate than Kurtén's because their's was derived from a single individual whereas Kurtén's value was calculated from composite measurements (e.g., femurs and tibias which came from different individuals). However, data from a single specimen from Indiana, measured by Richards and Turnbull (1995), and composite values from Beringia (this study), seem to confirm that Emslie and Czaplewski's value for *Arctodus* is lower than average and that their values for brown bears are somewhat high (Table 4). I believe these discrepancies have arisen because there can be a wide range in proximal-distal indices within a given species, and it is my experience that the variation seems to be most influenced by the specimen's age, as young mammals have relatively longer distal segments (unpublished data). I have observed, for instance, that the occasional R/H values over 90 in bears are found only in individuals less than a few years old, so Emslie and Czaplewski's (1985) value of 95 most likely comes from a very young, and thus atypical, specimen. This phenomenon, along with individual variation in index values has muddled the question of whether *Arctodus* had relatively long distal limb segments, and thus whether or not it was cursorial.

The above data indicate that *Arctodus* did not evolve significantly longer distal leg segments relative to Ursine bears or even its closer Tremarctine relatives. However, because such a strategy is

TABLE 4. Humeroradial (R/H) and Femurotibial (T/F) indices in *Arctodus* compared to other carnivores. (R/H index = radius length / humerus length X 100; T/F index = tibia length / femur length X 100).[1, 2]

Species (location)	(R/H index)	(T/F index)	Sample Size R/H, T/F	Source
Arctodus (various)	85.6	74.5	6/8, 7/8 [3]	Kurtén (1967a)
Arctodus (various)	86.1	74.9	13/13, 11/13	calculated from data in Richards *et al.* (1996)
Arctodus (Nevada)	78.2	71.4	1, 1	Emslie and Czaplewski (1985)
Arctodus (Indiana)	80.8	73.4	1, 1	Richards and Turnbull (1995)
Arctodus (Beringia)	84.2	78.9 [4]	4/4, 3/3	this study
Spectacled bear	83.4	73.9	4/4, 4/4	Kurtén (1966b)
brown bear	86.0	76.5	1, 1	Kurtén (1966b)
brown bear	88.4 (83.0 - 95.0)[4]	73.5 (70.4 - 75.1)[5]	9, 9	Emslie and Czaplewski (1985)
brown bear	87.7 (83.6 - 91.0)[4]	73.7 (71.1 - 77.0)[5]	5/5, 5/5	this study
polar bear	87.7 (87.0 - 88.8)[4]	74.6 (72.2 - 76.3)[5]	4/4, 4/4	this study
black bear	88.4 (82.8 - 90.2)[4]	78.2 (75.2 - 82.7)[5]	6/6, 6/6	this study
wolf	100.0	106.0	6, 6	this study
cheetah	103.3	105.0	6, 6	Gonyea (1976)
lion	98.3	90.6	6, 6	Gonyea (1976)
leopard	90.5	94.8	6, 6	Gonyea (1976)
tiger	89.8	90.1	7, 7	Gonyea (1976)
puma	89.5	99.6	6, 6	Gonyea (1976)

[1] Preferably, values should be calculated on limb elements from the same animal rather than composites of isolated bones. Since few paired elements exist for fossils, *Arctodus* values are calculated using average lengths for each bone. Index ranges are given when calculated on multiples of single individuals. Ranges do not exist for others because indices are calculated from composite averages or were not listed by authors.

[2] bone length = the greatest length parallel to the shaft

[3] Kurtén's sample size is presumably based on the number of samples listed in his various tables

[4] this value is probably too high because one of the three femurs was unusually small

[5] variation in ratios seems to be most associated with specimen age, as juveniles tend to have relatively longer distal segments (see text)

TABLE 5. Relative lengths of limb bones as a percentage of whole limb length in *Arctodus* versus other bears.[1]

limb element	short-faced bear[2]	short-faced bear (Kurtén)[3]	brown bear[4]	brown bear (Kurtén)[5]	polar bear[6]	black bear[7]	black bear (Kurtén)[8]	spectacled bear[9]	Florida cave bear[10]
humerus	47.6	48.2	46.2 (46.0-46.5)	47.5	46.8 (46.8, 46.8)	46.9 (46.4, 47.4)	46.4	48.5	48.9
radius	41.0	40.0	41.0 (40.3-41.6)	40.8	40.8 (40.7, 40.9)	41.7 (41.4, 41.9)	41.5	40.2	40.8
longest metacarpal[11]	11.5	11.8	12.8 (12.2-13.3)	11.7	12.4 (12.3, 12.5)	11.5 (11.3, 11.6)	12.0	11.4	10.3
femur	51.1	51.3	49.9 (49.7-50.2)	49.8	50.6 (50.3, 50.9)	50.2 (50.1, 50.2)	49.9	49.2	51.5
tibia	38.3	38.3	37.4 (36.8-38.3)	38.1	37.2 (36.7, 37.7)	38.8 (38.7, 38.9)	38.5	39.9	38.0
longest metatarsal[12]	10.6	10.5	12.6 (12.0-13.0)	12.1	12.2 (12.0, 12.3)	11.1 (11.0, 11.1)	11.7	10.9	10.5

[1] Ideally, values should be calculated from complete skeletons rather than composites of isolated bones. However, very few complete skeletons are available for most of these species. It is noted below whether values are from complete skeletons or composites.
[2] composite values calculated from averages of multiple single elements in Richards *et al.* (1996, appendix 2)
[3] composite values calculated from averages of multiple single elements in Kurtén (1967, Table 27)
[4] calculated individually on 3 complete brown bear limbs in the University of Alaska Museum (UAM 14784, 16559, 19765); average listed with range in parenthesis
[5] calculated from measurements in Kurtén (1966, Table 36) from a single, complete European brown bear
[6] calculated individually on 2 complete polar bear limbs in the University of Alaska Museum (UAM 16545, 16546); average listed with range in parentheses
[7] calculated individually on 2 complete black bears limbs in the University of Alaska Museum (UAM 3144, 14783); average listed with range in parentheses
[8] calculated from measurements in Kurtén (1966, Table 36) made on 5 separate individuals; Kurtén listed the resultant average but no other statistics
[9] calculated from measurements in Kurtén (1966, Table 36) made on a single spectacled bear
[10] composite values calculated from averages of multiple single elements in Kurtén (1967, Table 27)
[11] MC III in *Arctodus*; MC IV in other Tremarctines and all Ursines
[12] MT IV in Tremarctines; MT V in Ursines

unlikely to impart any significant energetic benefits to an animal with limbs that are distally heavy, this fact does not refute the notion that *Arctodus* had cursorial tendencies. Therefore, the next logical step is to look for ways that *Arctodus* may have been reducing distal limb weight— a feature one might see in a cursor early in its evolution.

Limb Mass and Allometry

Podials: Kurtén (1967a) suggests that, in general, the podials of *Arctodus* (e.g., scapholunar, navicular, calcaneum, pisiform) were built somewhat lighter compared to other Tremarctine and Ursine bears. This assertion and its implications for locomotion are difficult to quantify in a meaningful way. Nonetheless, even slight reduction in the weight of the feet may impart significant kinematic advantages because the feet's distal position amplifies the effect of their mass (Chapter 2). In terms of the cursorial debate, podial morphology (as summarized by Kurtén 1967a) weakly falls in favor of cursorialism.

Metapodials: In contrast, the metapodials of *Arctodus* do display a clear trend towards weight reduction— while they are absolutely longer than in other bears, they are relatively both shorter and more slender (shown by Kurtén 1966b, 1967a). Kurtén's (1967a) Table 16 and his Figs. 24 and 27 reveal how the allometry of *Arctodus*' metapodials is indeed transposed, indicating a Type II form of compensatory growth (see previous chapter's section on allometry). My calculations of width/length percentages from Kurtén's data indicate that this transposition reduces the relative width (thus density) of the metapodials. This value for width/length is 13.5 % for *Arctodus*, 17 % for brown bears, 20 % for cave bears, and 18 % for *T. floridanus*.

While *Arctodus*' metapodials are absolutely the longest among bears, they are not relatively longer for *Arctodus*' size or relative to its other limb bones (Table 5). Therefore, the slenderness of these bones is most logically interpreted as a weight-reducing measure. Kurtén apparently thought that their absolute length alone was evidence for cursorialism, but data in Table 5 show that the metapodials were not lengthened compared to relative lengths in other bears. Furthermore, the fact that all other long bones in *Arctodus*' limbs increased in relative length indicates that the metapodials may have been selectively shortened. This is consistent with the argument that *Arctodus* was in the initial stages of cursorial evolution in that it reduced limb weight, but not to the point where increasing distal limb length brought it any kinematic advantage. However, it should be pointed out that short metapodials seem to be the general trend for Tremarctine bears, as indicated by values in Table 5 for the spectacled bear (*Tremarctos ornatus*) and the extinct Florida cave bear (*Tremarctos floridanus*) — two bears which are justifiably considered to be non-cursorial (Kurtén 1966, 1967a, Kurtén and Anderson 1980).

Long Bones: I have quantified the gracileness of the limbs in *Arctodus* and other bears using the width:length ratio (W/L) of the five major limb bones (Table 5). Assuming equal densities and cortical

thickness, this index of gracileness functions as an indicator of relative limb weight. The results show that all four elements in *Arctodus* were significantly more gracile, and thus lighter, than in all species of *Ursus* when compared to each of these species individually or to the genus as a whole. This is even more significant considering the larger size of *Arctodus*; as per discussions in Part I, larger animals that engage in similar activities as smaller animals must evolve thicker bones in order to handle the increased stress. *Arctodus* did not do this; so, considering its size, it must have been incurring relatively lower stresses than modern bears.

Next I want to take a closer look at the allometries of the humerus, radius, ulna, femur and tibia in *Arctodus* compared to other bears of differing phylogenetic distance from *Arctodus*. This approach will help quantify the direction and extent of morphological divergence in *Arctodus*' limbs. For instance, was *Arctodus* simply a scaled up Tremarctine bear, or was it convergent on the Ursine body plan? Only in the latter case will it be justifiable to draw analogies about locomotion, ecology, and behavior between *Arctodus* and these more familiar bears. Furthermore, since it has been suggested that short-faced bears and brown bears became competitors in North America (Kurtén and Anderson 1974, 1980; Harington 1977, 1980; Richards *et al.* 1996), one might predict certain convergences in body shape. Kurtén's (1967) work left many of these questions about long bones unanswered or at least ambiguous, even though he made conclusions that are dependent on their answers.

In discussing these patterns of limb bone allometries, I will be referring directly to the data presented in Tables 6 and 7 and Figs. 15 - 19, as well as to concepts and terms discussed in the previous chapter's section on scaling and allometry. Note in particular that I only will be comparing lines of allometry for individual species, not higher taxa, as it is misleading for the considerations at hand to compare combined allometries— such as a comparison between the allometry of short-faced bears versus the combined allometry for all other Ursids (see reasons why in previous chapter). Also, I will wait to discuss the overall implications to locomotion until after summarizing the specific patterns in each bone. It was not always possible to obtain large sample sizes for every bone in every species, so some of the following conclusion could be challenged by larger data sets. For similar reasons, some tests of significance indicated in Tables 6 and 7 may be spurious, and I indicate where the data are ambiguous. Finally, I would point out that the following discussion exemplifies how difficult it is to reveal true functional meaning in bone proportionality by comparing just simple proportions (e.g., length vs. width) or just lines of allometry. Both need to be used together to examine the functional effects of the way bone proportionality changes with size, and that is what I attempt to do.

TABLE 6. Gracileness Index in long bones of Ursids measured as *least shaft diameter ÷ length X 100*

	humerus [1]			radius [2]			ulna [3]			femur [4]			tibia [5]		
species	$\bar{x}$	***n***	***SEE***	$\bar{x}$	***n***	***SEE***	$\bar{x}$	***n***	***SEE***	$\bar{x}$	***n***	***SEE***	$\bar{x}$	***n***	***SEE***
A. simus	9.0	10	.1694	5.4	8	.1071	5.5	11	.1385	8.8	15	.1250	10.1	13	.1524
T. ornatus	7.4*	4	.9569	5.3	4	.2245	4.6*	4	.1190	7.6*	4	.5233	7.5*	3	.0800
T. floridanus	9.0	7	.3795	6.1*	7	.1795	5.2	6	.1340	9.3*	9	.0970	9.0*	10	.2188
U. arctos	8.5*	11	.2937	5.3	6	.3570	5.2	4	.0510	8.1*	15	.2179	8.1*	5	.2846
U. maritimus	9.1	5	.2380	5.8	4	.2260	5.8	4	.0712	8.4	6	.2233	8.2*	4	.0997
U. americanus	8.5*	7	.1906	5.4	6	.1742	5.0*	7	.1599	8.0*	7	.1532	8.1*	6	.0959
Tremarctines [6]	8.7*	21	.2192	5.6	19	.1240	5.3	21	.1117	8.8	28	.1427	9.4*	26	.2001
Ursines	8.7*	23	.1543	5.5	16	.1585	5.3	15	.1204	8.2*	28	.1250	8.1*	15	.0984
combined Ursid [7]	8.7*	44	.1324	5.6	35	.0983	5.3	36	.0814	8.5*	56	.1024	8.9*	28	.1619
test of significance (P) in Tremarctinae vs. Ursinae	$P_{1\text{-tailed}} = .000$			$P_{1\text{-tailed}} = .000$			$P_{1\text{-tailed}} = .000$			$P_{1\text{-tailed}} = .001$			$P_{1\text{-tailed}} = .038$		

* index significantly different than *Arctodus* at $P_{1\text{-tailed}} \leq .05$, using t-test and assuming equal variance

[1] minimum transverse diameter of shaft

[2] minimum anterior-posterior diameter of shaft

[3] minimum transverse diameter of shaft above capitulum

[4] minimum shaft diameter in transverse plane

[5] minimum shaft diameter; can be in any plane

[6] values shown include *Arctodus*, but test of significance calculated as *Arctodus* versus the other two Tremarctines

[7] values shown include *Arctodus*, but test of significance calculated as *Arctodus* versus all other bears

TABLE 7. Linear ($y = ax + b$) and power ($y = bx^a$) functions for length (x) versus width (y) in long bones of Ursids. Power functions indicate lines of allometry where α equals the allometric constant. W/L ratio from Table 6 provided to indicate when a change of allometry may represents compensatory growth (see text and Fig. 6, previous chapter). Lines are plotted in Figs. 15 - 19. (Testing of H_0 is by Analysis of Variation for linear equations, and by Student's t-test for power equations.)

HUMERUS		**Linear Equation**				**Power Equation**				
species (n)	**W/L (Table 4)**	**equation**	**r^2**	**SEE (of y estimate)**	**P H_o: $a = 0$**	**equation**	**r^2**	**SEE (of slope)**	**$P_{1\text{-tailed}}$ H_o: $\alpha = 0$**	**$P_{1\text{-tailed}}$ Ho: $\alpha = 1$**
A. simus (10)	9.0	$y = .1196\,x - 13.9724$	.95	2.1483	.0000	$y = .0169\,x^{1.27}$	.93	.1232	.0000	.0293
T. ornatus (4)	7.4	$y = .1200\,x - 11.0569$	.65	2.3295	.1949	$y = .0009\,x^{1.80}$	.68	.8832	.0892	.2298
T. floridanus (7)	9.0	$y = .1056\,x - 6.0006$	.60	4.3914	.0417	$y = .0283\,x^{1.19}$	.67	.3756	.0124	.3145
U. arctos (11)	8.5	$y = .1286\,x - 12.5093$	.91	2.5315	.0001	$y = .0082\,x^{1.40}$	.91	.1624	.0000	.0178
U. maritimus (5)	9.1	$y = .1451\,x - 18.9985$	.92	1.3167	.0091	$y = .0023\,x^{1.59}$	.92	.2663	.0952	.0565
U. americanus (7)	8.5	$y = .0679\,x + 4.9906$	.66	1.5416	.0272	$y = 3.9039\,x^{0.81}$	.68	.2450	.2316	.2316

TABLE 7 (continued)

RADIUS		Linear Equation				Power Equation				
species (*n*)	W/L (Table 4)	equation	r^2	SEE (of *y* estimate)	*P* H_o: $a = 0$	equation	r^2	SEE (of slope)	$P_{1\text{-tailed}}$ H_o: $\alpha = 0$	$P_{1\text{-tailed}}$ H_o: $\alpha = 1$
A. simus (8)	5.4	$y = .0452\,x + 3.4752$	.72	1.3869	.0074	$y = .1369\,x^{0.84}$	.73	.2079	.0034	.2354
T. ornatus (4)	5.3	$y = .0731\,x - 4.0135$	.63	1.0768	.2070	$y = .0091\,x^{1.33}$	.62	.7426	.1076	.3501
T. floridanus (7)	6.1	$y = .0860\,x - 7.6395$	.89	1.1781	.0013	$y = .0054\,x^{1.42}$	.87	.2511	.0012	.0776
U. arctos (6)	5.3	$y = .1046\,x - 14.6531$	.98	0.8189	.0001	$y = .0004\,x^{1.87}$	.98	.1331	.0001	.0014
U. maritimus (4)	5.8	$y = .0933\,x - 10.6089$	.83	1.3200	.0897	$y = .0017\,x^{1.02}$	.85	.4766	.0392	.1615
U. americanus (6)	5.4	$y = .0823\,x - 7.0943$	.79	1.0274	.0170	$y = .0030\,x^{1.52}$	.84	.3372	.0054	.0989

ULNA		Linear Equation				Power Equation				
species (*n*)	W/L (Table 4)	equation	r^2	SEE (of *y* estimate)	*P* H_o: $a = 0$	equation	r^2	SEE (of slope)	$P_{1\text{-tailed}}$ H_o: $\alpha = 0$	$P_{1\text{-tailed}}$ H_o: $\alpha = 1$
A. simus (11)	5.5	$y = .0807\,x - 11.5234$	.87	1.7900	.0000	$y = .0043\,x^{1.42}$	.83	.2175	.0001	.0428
T. ornatus (4)	4.6	$y = .0304\,x + 3.8135$	.54	.5709	.2667	$y = .3119\,x^{0.65}$	.51	.4502	.1423	.2591
T. floridanus (6)	5.2	$y = .0927\,x - 13.2913$	.43	1.1396	.1542	$y = .0006\,x^{1.78}$	.44	1.0007	.0748	.2396
U. arctos (4)	5.2	$y = .0542\,x - .7731$	.96	3525	.0212	$y = .0355\,x^{1.07}$	.96	.1583	.0107	.3591
U. maritimus (4)	5.8	$y = .0571\,x + .4054$	.91	.5920	.0480	$y = .0625\,x^{0.99}$	.90	.2361	.0263	.4850
U. americanus (6)	5.0	$y = .391\,x + 3.0932$	.47	1.2518	.1340	$y = .1885\,x^{0.76}$	.48	.3960	.0628	.2886

TABLE 7 (continued)

FEMUR		Linear Equation				Power Equation				
species (*n*)	W/L (Table 4)	equation	r^2	SEE (of *y* estimate)	*P* H_o: $a = 0$	equation	r^2	SEE (of slope)	$P_{1\text{-tailed}}$ H_o: $\alpha = 0$	$P_{1\text{-tailed}}$ H_o: $\alpha = 1$
A. simus (15)	8.8	$y = .1054\,x - 9.4423$	.90	2.5168	.0000	$y = .0293\,x^{1.17}$	.89	.1156	.0000	.0826
T. ornatus (4)	7.6	$y = .1519\,x - 20.4205$	.57	2.9531	.2482	$y = .0003\,x^{2.02}$	.54	1.3068	.1314	.2584
T. floridanus (9)	9.3	$y = .1078\,x - 6.0827$	.95	1.1324	.0000	$y = .0361\,x^{1.10}$	.96	.0947	.0000	.0675
U. arctos (15)	8.1	$y = .1048\,x - 9.6964$	.82	3.1664	.0000	$y = .0160\,x^{1.27}$	.80	.1759	.0000	.0744
U. maritimus (6)	8.4	$y = .1030\,x - 8.1830$	.81	2.5452	.0135	$y = .0190\,x^{1.24}$	.83	.2766	.0054	.2173
U. americanus (7)	8.0	$y = .1061\,x - 8.340$	.87	1.2658	.0020	$y = .0133\,x^{1.31}$	.90	.2000	.0006	.0909

TIBIA		Linear Equation				Power Equation				
species (*n*)	W/L (Table 4)	equation	r^2	SEE (of *y* estimate)	*P* H_o: $a = 0$	equation	r^2	SEE (of slope)	$P_{1\text{-tailed}}$ H_o: $\alpha = 0$	$P_{1\text{-tailed}}$ H_o: $\alpha = 1$
A. simus (13)	10.1	$y = .1331\,x - 13.5728$	.94	1.7445	.0000	$y = .0140\,x^{1.33}$	.93	.1117	.0000	.0066
T. ornatus (3)	7.5	$y = .0452\,x + 6.2817$	.87	.2053	.2339	$y = .6398\,x^{.60}$	.86	.2377	.1202	.1672
T. floridanus (10)	9.0	$y = .1600\,x - 20.0259$	.93	1.1632	.0000	$y = .0015\,x^{1.72}$	.92	.1811	.0000	.0020
U. arctos (5)	8.1	$y = .1315\,x - 13.3426$	.83	1.5289	.0320	$y = .0031\,x^{1.58}$	.81	.4373	.0182	.1383
U. maritimus (4)	8.2	$y = .0677\,x + 4.3681$	.95	1.2964	.0276	$y = .2156\,x^{0.83}$	.94	.1523	.0160	.1902
U. americanus (6)	8.1	$y = .0926\,x - 3.0291$	.86	.6255	.0072	$y = .0307\,x^{1.17}$	.87	.2225	.0031	.0101

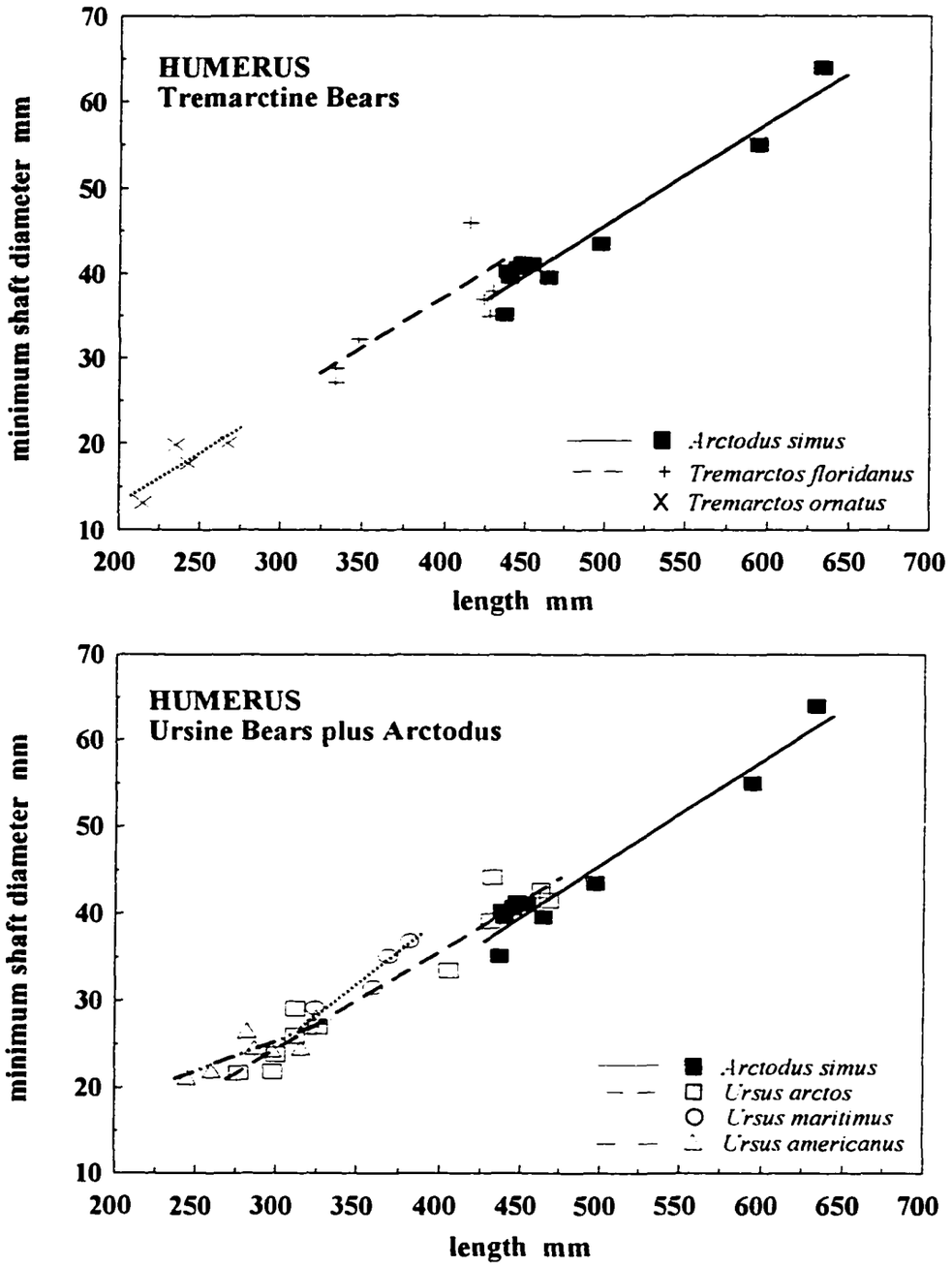


FIGURE 15. Humerus allometry in bears. Line formulas located in Table 5. Minimum diameter is in transverse plane. *Discussion in text.*

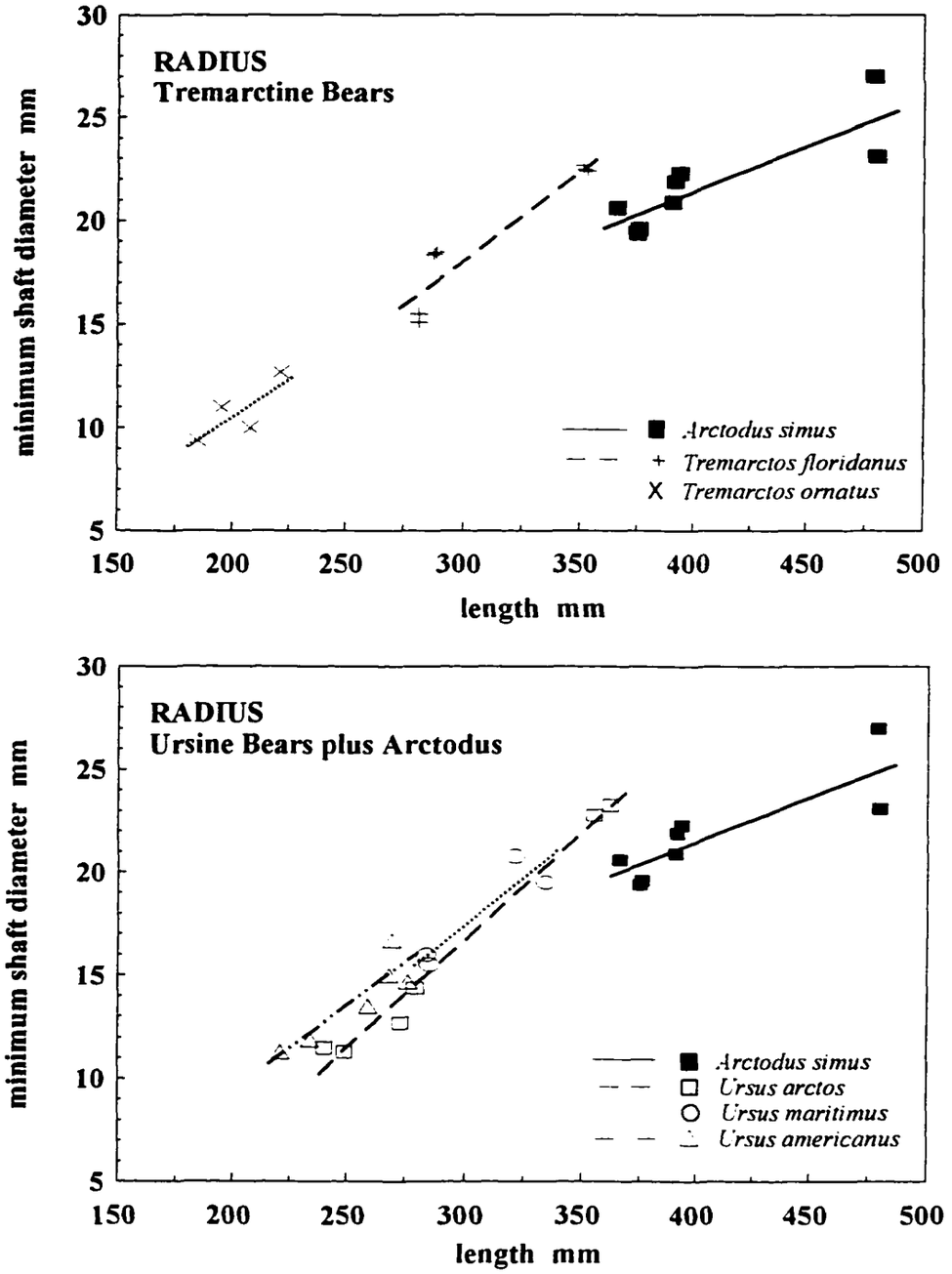


FIGURE 16. Radius allometry in bears. Line formulas located in Table 5. Minimum diameter is in anterior-posterior plane. *Discussion in text.*

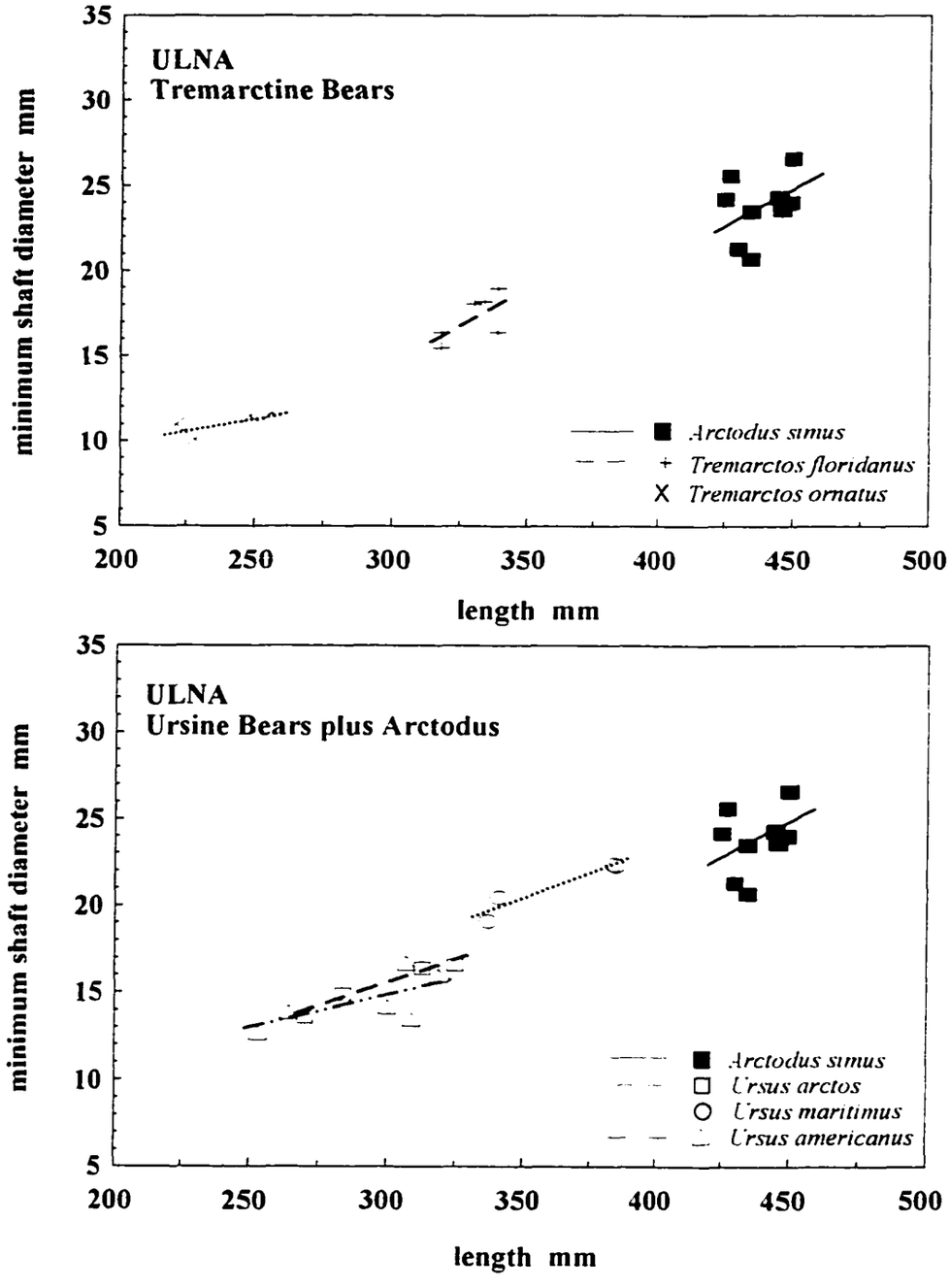


FIGURE 17. Ulna allometry in bears. Line formulas located in Table 5. Minimum shaft diameter is least transverse diameter above the capitulum. *Discussion in text.*

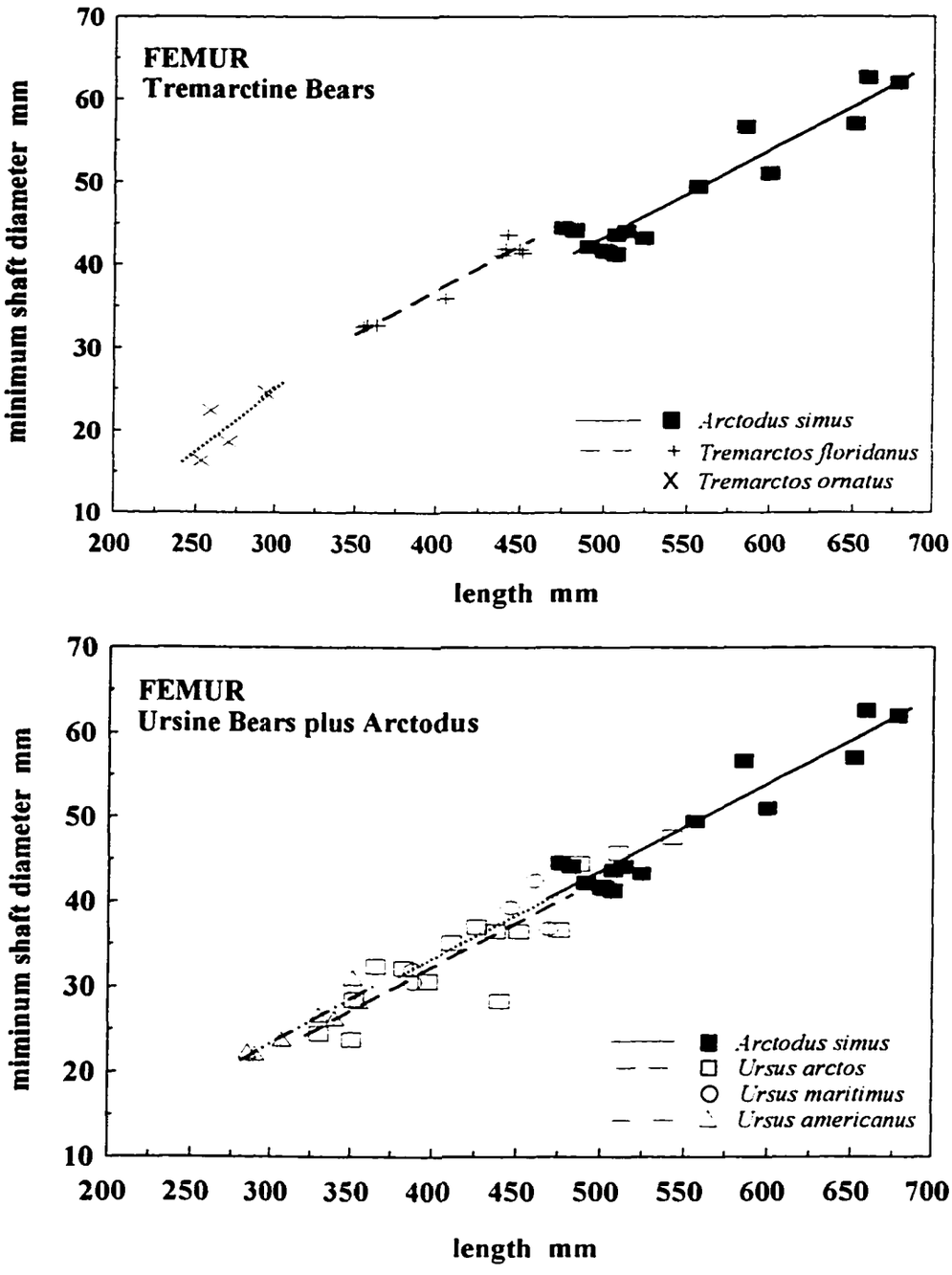


FIGURE 18. Femur allometry in bears. Line formulas located in Table 5. Minimum diameter is in transverse plane. *Discussion in text.*

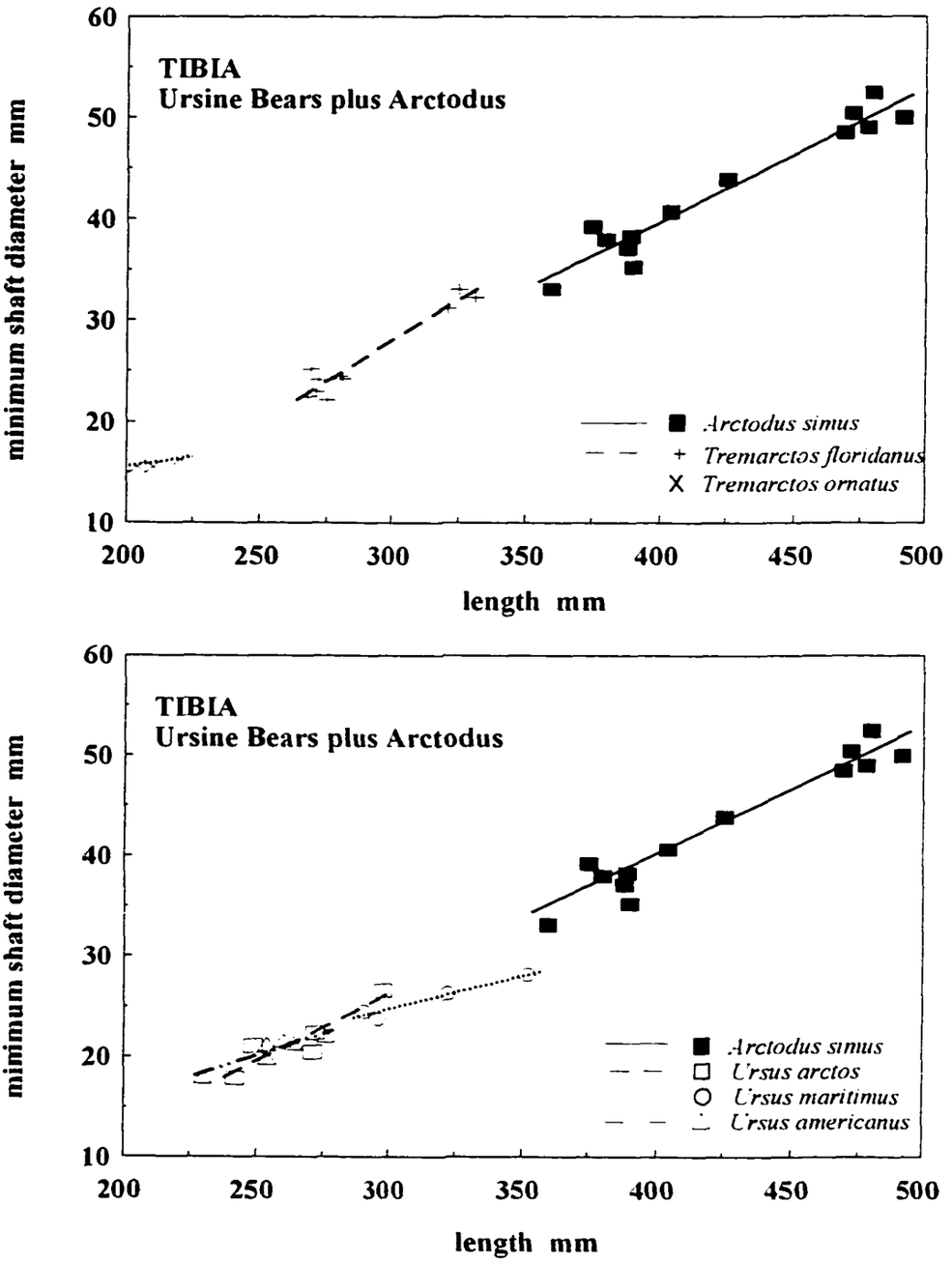


FIGURE 19. Tibia allometry in bears. Line formulas located in Table 5. Minimum diameter along shaft can be in any plane. *Discussion in text.*

HUMERUS (Fig. 15): Compared to its Tremarctine relatives, *Arctodus* displays a classic form of Type I compensatory growth in its humerus (recall that compensatory growth compensates for size, not function). Slopes for all three Tremarctines are over 1.0, and without some form of relative compensation, *Arctodus*' humerus would be hugely robust. The transposition in its allometry effectively gives it a somewhat similar proportionality (W/L ration of 9.0) compared to the other two Tremarctines, despite its size. But in order for *Arctodus* to withstand similar (scaled up) dynamic forces of locomotion as a smaller bear, it should be built relatively more robustly. Since it had a relatively weaker humerus for its mass, *Arctodus* must not have been experiencing equivalent levels of force or running in a similar fashion as *T. ornatus* or *T. floridanus*.

The same sort of pattern holds true when the humerus of *Arctodus* is compared to Ursine bears. In fact, Ursine and Tremarctine humeri vary little in proportions or allometry, with the exception of short-faced bears and perhaps polar bears. Short-faced bears show the most reduction in relative strength and weight of all bears, while polar bears seem to have unusually robust humeri, although the sample size for polar bears is small in this study.

RADIUS/ULNA (Figs. 16, 17): *Arctodus*' radius allometry departs strongly from the Tremarctine plan. It is both transposed and has a very low α (< 1); both reduce W/L, making it a very gracile bone in *Arctodus*. Because $\alpha < 1$, the radius in *Arctodus* actually gets progressively more gracile with increasing size. The relationship between the radii of *T. floridanus* and *T. ornatus* displays a good example of size enlargement without a compensatory change in growth. The α of the radius in these two species are not significantly different from each other (Student's t-test$_{2\text{-tailed}}$ $P = 0.280$), but their absolute W/L ratios are different (Student's t-test$_{2\text{-tailed}}$ $P = 0.036$). Effectively, extending *T. ornatus*' line of allometry into the size range of *T. floridanus* gives the latter bear a very robust radius— the widest of all bears tested. The compensatory allometry of *Arctodus* (both Type I and II) produces proportions of the radius (mean W/L = 5.4) more in line with the diminutive spectacled bear. For a bear the size of *Arctodus*, this extreme gracileness would make for a relatively much lighter and weaker radius.

In order to make a definitive functional assertion about the radius, data are needed on the ulna, since it is possible that any reduction in the radius is compensated for by strengthening the ulna. Data on Tremarctine ulnae show that this bone does indeed get absolutely more robust with size; mean W/L is 4.6 in *T. ornatus* but reaches 5.3 in *T. floridanus* and 5.5 in *Arctodus*. However, the radius and ulna both are robust in *T. floridanus*, and the two bones have parallel proportions in *T. ornatus*, meaning these two species probably had forearms with comparable strength, weight, and performance relative to their size. In *Arctodus*, however, only the ulna remains proportionally stout, but in my estimate, not enough so to completely compensate for the light radius; the forearm of *Arctodus* thus appears to have been more gracile and differed functionally from other Tremarctines.

The allometry of *Arctodus*' radius also deviates strongly from Ursine bears, and in a way similar to its deviation from Tremarctines. In fact, with the exception of *Arctodus*, Ursine and Tremarctine allometries are quite similar for the radius. Values for α tend to be higher in Ursines, so their radii get somewhat stronger and heavier in larger individuals of a given species compared to Tremarctines, but *T. floridanus* stands out because of its high absolute W/L ratio. The relative transposition of *Arctodus*' allometry and its extremely low α give this largest of bears nearly the lowest mean W/L for its radius. Considering the increased static and dynamic forces commensurate with its size, *Arctodus*' radius was substantially lighter and weaker than that of all other bears.

I showed that the ulna of *Arctodus* did not increase proportionately with size to compensate for a lighter radii, whereas it did in other Tremarctines. The same pattern essentially holds true when *Arctodus* is compared to Ursines. Bear ulnae in general have low α values compared to other long bones, and while it seems that this bone increases in robustness with size at a fast rate in *Arctodus* (i.e., high α) this trend probably is not as strong as its appears. I make this statement because the data in Fig. 17 (and the statistics in Table 7) show that there is considerable variation in ulnae proportions within a species, especially *Arctodus*, and the apparently high α (1.42) in *Arctodus* is just barely statistically distinct from 1 ($P = 0.0428$) Overall, the forearm of *Arctodus* was not a scaled up version of any bear in consideration, nor does its allometry compensate (functionally) for its large size— both the radius and ulna of *Arctodus* were relatively weak and light.

FEMUR (Fig. 18): Like the humerus, the femur allometry of *Arctodus* exhibits a clear transposition compared to the other two Tremarctines. And since the absolute proportion (W/L) of *Arctodus*' femur is significantly less than that of the other two, the arguments presented for the humerus also apply here, but even more so— the femur of *Arctodus* was absolutely, and especially relatively, lighter and weaker than that of its closest relatives.

Functionally, one gains better insight into the proportions of *Arctodus*' femur by comparing it to that of the more familiar Ursine bears, where the pattern does not parallel the humerus. Here, one finds that *Arctodus*' femur is practically indistinguishable from the larger Ursines. Mean W/L and α of *Arctodus* are not statistically distinct from polar bears, but more importantly, there is not much difference in femur proportions between large brown bears and small short-faced bears (see area of overlap in Fig. 18). *Arctodus* shows significant allometric transposition only from the much smaller black bears, as one would expect— but even here the deviation is less than it is between *Arctodus* and its closest small relative, *T. ornatus*. Thus, the femur of short-faced bears converges with the Ursine plan, and since there is a substantial zone of size overlap between *Arctodus* and very large Ursines, it would be difficult to argue that the bending strength of their femurs was much different. The fact that mean W/L in *Arctodus* is greater than in Ursines argues that femur proportions in short-faced bears maintained similar strength

despite their large size (i.e., they retained the same relative strength). Morphological convergence with Ursines does not necessarily imply functional convergence, even though it can be concluded that bending strengths were roughly similar between these distantly related bears. After summarizing data on the tibia, where a similar pattern arises, I will discuss possible reasons for this convergence and suggest a reason why the bones of *Arctodus'* hind limbs were heavily built whereas its front limbs were lightly built.

TIBIA (Fig. 19): Mean W/L is 10.1 in *Arctodus*, but only 9.0 in *T. floridanus* and 7.5 in *T. ornatus*, so in absolute terms *Arctodus'* tibia is quite robust compared to its Tremarctine relatives. Concordantly, its line of allometry is only slightly transposed (sample size is too small for *T. ornatus* to produce a reliable regression line, so this statement is made upon visual inspection and in comparison to *T. floridanus*). *Arctodus'* line of allometry for its tibia is only slightly transposed compared to other Tremarctines, and since all α values are essentially greater than 1 in this group (sample size is too small in *T. ornatus* to tell for certain), this demonstrates a lack of compensatory growth. As a result, the tibia of short-faced bears is relatively wide. The tibia is the only long bone in *Arctodus* which is truly more robust than in other Tremarctines, and therefore it must have been functionally stronger (relatively) and heavier.

Compared to Ursine bears, *Arctodus'* tibia is absolutely more robust and its line of allometry displays practically no compensation, similar to the patten seen in its femur. The fact that its line of allometry seems to be an extension of the brown bear's line adds to the suggestion that the tibia in *Arctodus* was a strong bone, functionally on par with other bears, even considering its size. I would conclude that selection in *Arctodus* was for a strong tibia.

OVERALL ALLOMETRY AND FUNCTIONAL INTERPRETATIONS: In terms of the cursorial debate, the overall allometric trends and absolute limb dimensions in *Arctodus* demonstrate that this very large bear reduced the relative weight and strength of its limb bones, compared to both its closest relatives (Tremarctine bears) and the more familiar Ursine bears. Some of these changes were implemented through compensatory growth, in which case the absolute proportions of *Arctodus'* limb bones are not much different than other bears. In the previous chapter, I emphasized that as geometrically similar animals get larger (i.e., even those with compensatory growth), dynamic and static stresses in their bones increase faster than bone's ability to dissipate these forces. Therefore, geometrically similar animals of greatly different size cannot perform in geometrically similar ways; larger animals must curtail high force activities, or have bones that are relatively thicker. So while evidence such as limb weight reduction suggests that *Arctodus* was evolving cursorial tendencies, it does not seem plausible that this bear was built to withstand the high forces of fast running and predation.

An important pattern to note in the limbs of *Arctodus* is that although this species did not evolve longer distal segments, it did reduce distal mass, especially in the front limbs. This is indicated by the highly transposed allometry of the radius and lack of compensatory growth in the ulna (earlier I noted that

the metapodials of *Arctodus* also are relatively lighter). Previously, I commented that it is not logical to predict increased distal limb length in a cursorial bear because bear feet are so heavy, giving the limbs considerable distal weight. It is logical, however, to expect such a bear to reduce distal weight— and that is what *Arctodus* did.

Dimensional data showed that the hind limb bones of *Arctodus* are somewhat more robust (shorter and heavier) than its front limb bones. I believe this pattern is easily explained by the relative lengths of these bones. Table 8 presents data for the absolute and relative lengths of the major limb bones and axial segments of *Arctodus* and other bears discussed in this chapter. Table 9 shows two indices calculated from these data— Back Length Index (BLI) and Intermembral Index (IMI)(Fig. 20). BLI is calculated as the length of the thoracic and lumbar regions divided by the combined lengths of the four major limb bones; IMI is calculated as the combined length of the humerus and radius divided by the combined length of the femur and tibia [2]. These data primarily will be used later in discussions on gait selection, but here I use them to point out how the IMI of *Arctodus* reveals that its front limbs were relatively much longer than its hind limbs. In terms of limb allometries and gracileness, changing limb bone lengths without changing patterns of relative growth will have obvious impacts on W/L values and allometric parameters. Simply shortening the hind limbs will make them relatively more robust and lengthening the front limbs makes them relatively more gracile. Kinematically, the relatively robust hind limbs of *Arctodus* would not have been disadvantageous since they were short, meaning the mechanical encumbrance of their weight was minimal.

It is puzzling to note that both Kurtén (1967a) and Baryshnikov *et al.* (1994) conclude that *Arctodus* had relatively long hind limbs and relatively short front limbs compared to other bears. The data for IMI in Tables 8 and 9 and Fig. 20 clearly indicate that *Arctodus* was relatively tall in the shoulders and short in the hind quarters (also see Fig. 4a, previous chapter, which shows an accurate reconstruction of *Arctodus'* skeleton using skeletal data presented here). In Kurtén's case, I can only suggest that this conclusion was the result of using composite measurements for limb lengths in *Arctodus* (he used complete skeletons of modern species for comparison). At the time of his study, no complete skeletons of *Arctodus* were available (the data for the various bear species in Table 8 are all from single individuals). Kurtén reported lengths for the front and hind limbs as percentages of presacral length (lumbar, thoracic, and cervical vertebrae plus skull length), but as noted in footnote 8 of Table 8, he erred in his calculation of axial segment lengths for *T. floridanus* and *T. ornatus* (his values are too high). While this error does not affect comparisons of front and hind limb length, it does give the impression that the legs were shorter

[2] Length of each vertebral region was determined by measuring the anterior-posterior width of individual centra at their widest point and summing these widths for each region. Length of long bones was measured as the greatest length parallel to the long axis of the shaft.

TABLE 8. Absolute and relative lengths of limb and axial segments in *Arctodus* versus other bears[1]. See Table 6 for comparison of BLI and IMI in these bears and other carnivores.

element(s) [2]	short-faced bear [3] PM 24880	short-faced bear (Kurtén) (females) [4]	brown bear [5]	brown bear (Kurtén)	polar bear [6]	black bear [7]	spectacled bear [8] (Kurtén) miss-calculated	spectacled bear (Kurtén) actual	Florida cave bear [4] (Kurtén) miss-calculated	Florida cave bear (Kurtén) actual
humerus (H)	594	—	304	357	369	321	235	235	—	—
radius (R)	480	—	273	307	321	278	195	195	—	—
femur (F)	651	—	352	395	446	355	259	259	—	—
tibia (T)	478	—	271	302	322	279	210	210	—	—
IMI [9]	95	—	93	95	90	94	92	92	—	—
cervical vertebrae (c)[10]	238	181.5	148	169.4	214.6	122.4	*163.7*	115.1	*288*	214.7
thoracic vertebrae (t)	584	538	360	425.5	522.6	398.4	308.4	308.4	472.0	472.0
lumbar vertebrae (l)	426	367.7	267	304.0	381.3	313.6	225.1	225.1	324.0	324.0
c + t + l	1248	1087	775	898.9	1118.5	834.4	*697.2*	648.6	*1384.0*	1010.7
c / c + t + l X 100	19.1	16.8	19.1	18.8	19.2	14.7	*23.5*	17.7	*26.6*	21.2
t / c + t + l X 100	46.8	49.5	46.5	47.3	46.7	47.7	*44.2*	47.5	*43.6*	46.7
l / c + t + l X 100	34.1	33.8	34.5	33.8	34.1	37.6	*32.3*	34.7	*29.9*	32.1
BLI [11]	46	—	53	54	62	58	59	59	—	—

[1] The most accurate values will be derived from complete skeletons, not composite measurements from separate individuals. Values for short-faced bear, brown bear, polar bear, black bear, and spectacled bear are from complete skeletons. Kurtén's (1967) values for Florida cave bear are composites, but fairly accurate because they are derived from several nearly complete skeletons. NOTE: Kurten's (1967, Table 9) values for axial composition include skull length, which is not included in this table; his values presented here have been adjusted to reflect this difference.

[2] vertebral lengths measured as greatest anterior-posterior length of centra; these lengths should not be taken to be actual lengths because they do not account for vertebral discs or spinal flexure.

[3] data calculated from PM 24880 in Richards and Turnbull (1996), several vertebrae missing, missing centra depths estimated from neighboring vertebrae; PM 24880 is a very large-bodied specimen.

[4] data from Kurten (1967).

[5] UAM 14784, University of Alaska Museum. [6] UAM 16545, University of Alaska Museum. [7] UAM14783, University of Alaska Museum.

[8] Table 9 in Kurtén (1967) reports relative lengths of axial segments for *T. ornatus* and *T. floridanus* based on raw data in Kurtén (1966); inspection of Kurten's raw data reported for AMNH 2861 shows that he miscalculated the total for cervical vertebrae length. This total, when calculated directly from raw data in Kurten's (1966) Table 8 is much lower than his total listed in Table 12. Apparently, his value in Table 12 includes the axis and atlas, which he excluded for other bears when calculating percentages in the 1967 paper's Table 9. The result is that his proportions for the neck are too high and those for the thoracic and lumbar are too low. As a result, Kurten's conclusion that *T. floridanus* and *T. ornatus* were relatively longer necked than *Arctodus* is incorrect.

[9] IMI (Intermembral Index) = H + R / F + T. [11] BLI (Back Length Index) = t + l / H + R + F + T.

[10] cervical portion does not include axis and atlas, for consistency with Kurten (1966, 1967).

TABLE 9. Intermembral Indices (IMI) and Back Length Indices (BLI) for *Arctodus* and other large carnivores discussed in text

	IMI[1]			
species	$\bar{x}$	***range***	***n***	**BLI[2]**
spotted hyena[3]	98	95 - 101	8	49
short-faced bear	96	95 - 96	2	46
black bear	93	88 - 97	6	58
brown bear	92	90 - 93	4	52
wolf	91	90 - 92	6	54
spectacled bear	90	84 - 95	4	59
polar bear	89	87 - 90	4	62
lion[3]	86	83 - 88	10	63

[1] IMI = humerus length + radius length / femur length + tibia length x 100

[2] BLI = thoracic length + lumbar length / humerus length + radius length + femur length + tibia length x 100; values reported taken on single individuals for which complete vertebrae were available (bears are same specimens as in Table 8), but are corroborated by measurements from photos

[3] data on lion and hyena from photos and scale drawings; values are less precise, but checks on data for bears and wolves confirm that accurate measurements can be made using this technique

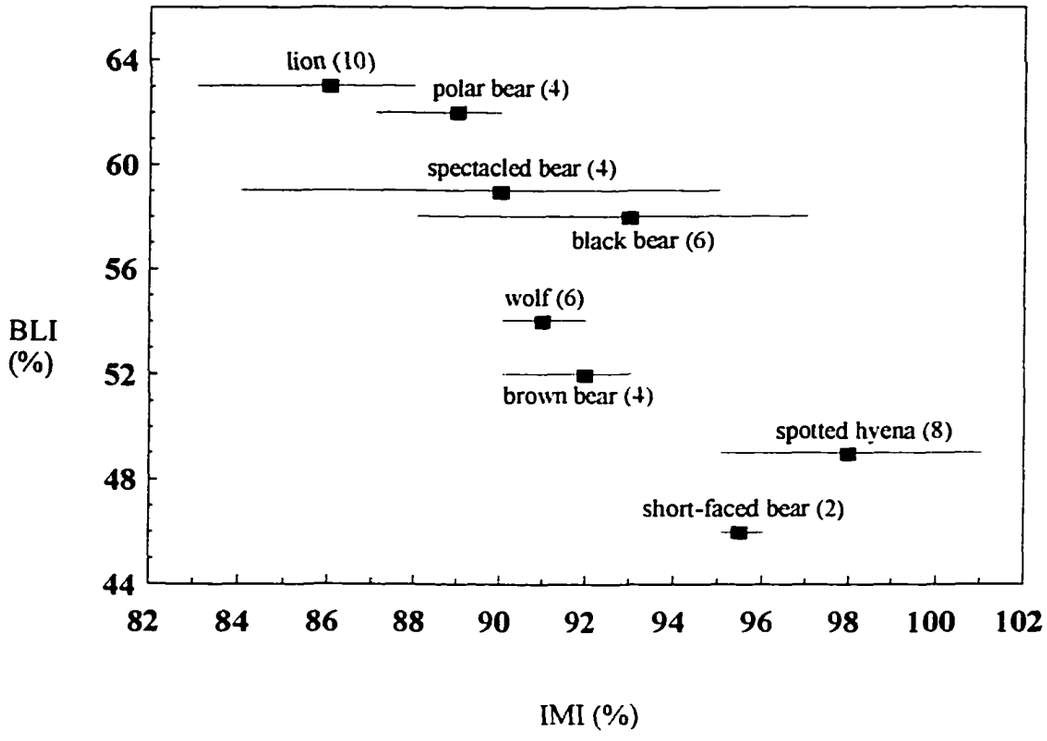


FIGURE 20. Back Length Index (BLI) and Intermembral Index (IMI) for short-faced bears compared to other bears and selected carnivores (plotted from data in Table 9). While short-faced bears were long-legged overall, the high IMI shows how their front legs were elongated the most, and that the hind legs were relatively short. The BLI reveals that the backs of short-faced bears also were short relative to leg length. In fact, their proportions are most similar to spotted hyenas. Large mammals with this type of conformation, especially those with high IMIs, use a pace as their mid-range gait because there is so much disparity between front and hind limb lengths. Of the species depicted, spotted hyenas are pronounced pacers, while the other species rarely pace. Pacing is an efficient gait for prolonged locomotion, and it is argued that short-faced bears were adapted for efficient long-range travel using such a gait. Species which accelerate well, such as felids, have relatively longer hind limbs (low IMI), which short-faced bears lacked. (sample sizes in parentheses; bars represent ranges of values for IMI; ranges not listed for BLI because actual vertebral lengths were only measured in bears-- in other species, back lengths were estimated from photos and lack the precision to warrant range bars.)

than they actually were in these two bears. The error also led Kurtén to the erroneous conclusion that the neck of *Arctodus* was substantially shorter than in these two relatives. Neck length, as a proportion of vertebral length, is about the same for all Tremarctines and does not differ much from Ursines (Table 8).

It is not clear how Baryshnikov *et al.* (1994) came to their conclusion about relative limb length in *Arctodus*, since the only surviving long bone in the specimen they studied was a single tibia. They do not cite data from other specimens or discuss comparative lengths of any limb bones in bears other than for the tibia. It is impossible to make a conclusion about intermembral ratios with data on only a single limb element, yet they state that, "the length of the hind leg bones indicate [*sic*] the animal was high in the hind quarters, not lowered as in *Ursus spelaeus*." (p. 350). Regarding their conclusion that *Arctodus* was a scavenger, but poorly adapted for this niche, these authors also make the statement that, "These limbs and locomotion are satisfactory for a scavenger." (p. 350), which would imply that selection for locomotor abilities necessarily will be lax in a scavenger. In the next chapter I present energetic and ecological arguments why there would be strong selective pressure on a large-bodied scavenger to evolve certain locomotor features, particularly the ability to cover large home ranges with maximum efficiency, contrary to the non-selectionist position of Baryshnikov *et al.* (1994).

Indeed, the relative changes in front and hind limb proportions of *Arctodus* compared to other bears have important functional implications. The disproportionately long front limbs would have generated larger bending moments, yet their gracileness meant they had less resistance to bending strains, relative to other bears. This means the front limbs could not withstand scaled up dynamic forces of locomotion on par with other bears. On the other hand, this change made the front limbs relatively lighter and kinematically less costly to oscillate. In later sections I will talk about how the long front limbs facilitated gait dynamics which also increased efficiency. There I will show that gait dynamics also explain the advantage of short hind limbs. The robustness of *Arctodus*' hind limbs is relative, and only stands out in comparison to the gracileness of the front limbs. The femur, for instance, is still less robust than in *T. floridanus* and has proportions similar to those of Ursine bears. Because the hind limb bones were relatively shortened, and thus lighter overall, it would be difficult to argue that their robustness was kinematically disadvantageous. This is especially true if they oscillated at slow to moderate speeds because the kinematic effect of limb mass increases exponentially with speed. Also, because bones of the hind limbs were not lengthened as much as those of the front limbs, their distal mass would not have been such a kinematic encumbrance. Therefore, their greater robustness adds little additional energetic costs at low speeds.

I think that last statement is the real key to understanding the type of cursorialism displayed by *Arctodus*. Since I showed evidence of cursorial modifications in *Arctodus*, but not a specific reduction in distal mass, this pattern suggests that *Arctodus* most likely was adapted for prolonged travel at moderate

speeds, not for sustaining high speeds. In previous chapter's section on kinematics, I discussed how the energy required to oscillate a given mass and the force required to accelerate it are a product of its velocity and its length down the limb. In a cursor built for sustained, but not fast locomotion, distal weight is not as critical in determining the limb's efficiency— because the velocity of distal masses is kept low, and the momentum which needs to be overcome four times per stride is much lower. For a cursor of this type, the real key is limb length; increasing stride length is by far the most effective way to increase efficiency. However, the mass of the entire limb is still an important factor in the energetic (kinematic)equation and the overall weight reduction of the entire limb is most logically interpreted as a means to reduce the energy required to swing the limb as a whole. Therefore, the key feature in the cursorialism debate in *Arctodus* lies with the fact that the entire limb, not just the distal ends, had evolved to be lighter. Combined with its long legs, this pattern indicates that *Arctodus* had evolved for sustained high-efficiency locomotion at moderate speeds, where the kinematic effects of distal weight are not so pronounced. Indeed, cursorialism is primarily about efficiency of energy use and sustainability of locomotion at a given speed; it is not principally about increasing speed.

Critics may contend that all of these adaptations in *Arctodus*' limb morphology would also be adaptive for sustaining high speed and thus for predation. But this cannot be the case because of its extreme mass. *Arctodus'* long, gracile front limbs would not have been strong enough to handle the forces of very high speed travel in such a large mammal, and, even if capable of sustaining high speeds, these legs would have been too weak to handle sudden force changes incurred during acceleration and maneuvering at high speeds— forces typically incurred by a predator. I would challenge proponents of the predatory model to demonstrate how such a "straight-line runner" could be a successful predator, or how *Arctodus*' specific morphology fits a particular predatory strategy. It would be contradictory for a cursor the size of *Arctodus*' to have such gracile limbs (or more precisely, to not have robust limbs) if its cursorial style was characterized by high force locomotion involving rapid acceleration and maneuvering at high speeds.

Limb Posture and Conformational Features

In addition to limb mass and proximal-distal limb proportions there are other skeletal indicators in *Arctodus* which attest to its cursorialism. These features primarily involve modifications to limb posture, which either reduce the energy of oscillation or decrease lateral leg excursion during a stride. Both of these modifications potentially increase locomotor efficiency, but could also increase the velocity of limb oscillation.

Compared to amblers, cursors swing their legs in a more parasagittal plane (parallel to the body), and their foot path tends to follow a nearly straight line that circumscribes a narrow horizontal ellipse or

figure 8 on the ground (Jenkins and Camazine 1977) (Fig. 21). The limbs of less cursorially adapted mammals are swung with considerable lateral migration (abduction) during a stride, thereby traveling through a wider ellipse or figure-8 pattern (particulary in the hind limbs). Unlike cursors, the body's mass is lifted little during the stride of amblers, which is partially why amblers do not swing their hind limbs under the body so much as to the sides (Jenkins and Camazine 1977; Hildebrand 1985a, 1995). Consequently, their femurs are positioned in a more abducted (laterally splayed) position and there is considerable lateral pelvic rotation during a stride. This primitive pattern of motion would be inefficient at higher speeds or for prolonged travel, so more cursorial species have made significant modifications to this plan (Hildebrand 1976, Jenkins and Camazine 1977). Joint angles (particularly the knees) in cursors also are more aligned with the sagittal plane, allowing the limbs to swing under the body simply by flexing them (i.e., without being swung laterally) (Jenkins and Camazine 1977, Hildebrand 1995).

The advantage of moving the limbs through a straight and parasagittal plane is twofold. First, the feet travel a shorter overall distance because there is less lateral migration. This reduces the energy needed to swing the limbs, increasing efficiency and endurance, but it also can increase the animal's speed since a limb which travels a shorter overall distance completes its stride more quickly. Second, fewer muscle groups, and thus less energy, are needed to swing a limb when it follows a parasagittal trajectory because skeletal mechanisms rather than muscles can be employed to constrain the direction of limb movement (Chapter 2, Section 4). This process increases efficiency and endurance but probably does little to directly enhance speed. But, since muscle mass is reduced, it has the added effect of making the limb lighter, and, as I showed in Chapter 2, this can help increase top speed and acceleration in some animals (mainly small to medium ones less than about 100 kg). It also should be noted that nearly all of these modifications which restrict abduction and adduction of the limbs will limit their use for other dextrous functions.

With the preceding considerations in mind, I will examine whether *Arctodus* displays cursorial modifications to its limb posture and line of travel. First, I will make a brief qualitative assessment of *Arctodus*' anterior limb conformation, followed by a more detailed evaluation of its hind limbs and pelvis using quantitative indicators of locomotor style. The hind limb assessment will include comparisons to other carnivores with diverse locomotor habits ranging from racoons and modern bears (two non-cursorial carnivores) to felids and canids, two cursorial carnivore morphs which use their limbs quite differently.

a. Front Limbs:

Earlier, I showed that, compared to other bears, *Arctodus* had evolved long front limbs relative to its hind limbs. Now, I want to show that the conformation of its front limbs differed from other bears and that *Arctodus* must have swung its front limbs quite differently than contemporary bears. Evidence for these conclusions comes from the morphology of *Arctodus*' ribs and thoracic cavity. Richards and

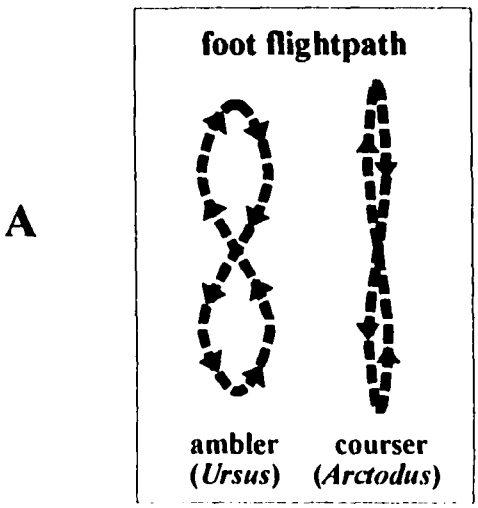
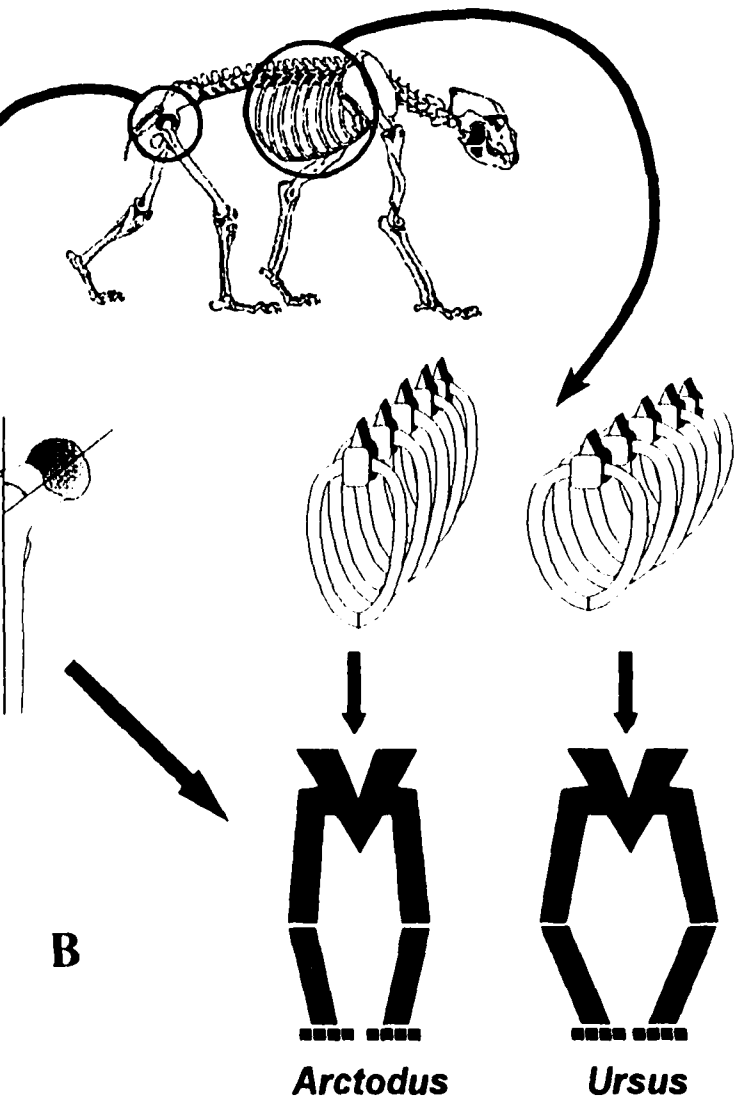


Figure 21. Schematic of some cursorial features in *Arctodus* compared to *Ursus*. *A* The foot flightpath of amblers, such as *Ursus*, circumscribes a wide figure 8, which is less efficient but a necessary accommodation for a wide body and a steady, wide-legged stance. Coursers, such a *Arctodus*, swing their legs in a tighter figure 8 or even an ellipse. This flightpath is energetically more efficient, but can be potentially unstable. *B* The conformation of the front and hind limbs and girdles in *Arctodus* allowed it to position its limbs more medially and to swing them in a more parasagittal plane compared to *Ursus*. The thoracic cavity was tall and narrow and widest at the 10th rib, as opposed to the 9th in Ursines. This latter feature means the widest part of the thoracic cavity was located more posteriorly in *Arctodus*, allowing the front limbs to take longer strides without significant lateral splaying. Reduced lateral splaying in the hind limb is brought about partially by a more acute angle in the neck of the femur and less medial-lateral bowing in the femur shaft.


B
Arctodus
Ursus

Turnbull (1995) and Kurtén (1966b) provide measurements on ribs in *Arctodus* and other bears. Their data show that the ribs of *Arctodus* had less bowing and were relatively longer than in other bears, indicating that its chest was deeper and narrower. In addition, the 10th rib is the longest of the series in *Arctodus*; normally the 9th rib is longest in bears. Therefore, the chest's greatest depth was more posteriorly located. Functionally, these features of the thoracic cavity would have positioned *Arctodus*' front limbs more medially (closer together) and thus more directly beneath its body. The limbs also could have been swung farther posteriorly before flaring laterally, since the largest part of the chest was most posterior (Fig. 21). The locomotor advantages of these traits are that: 1) the front limbs could be swung in a near parasagittal plane more parallel to the body; by reducing lateral excursion in the front limbs, the feet circumscribed a tighter ellipse, 2) effective stride length could be increased, and 3) placing the limbs more directly beneath the body increases the stability of lateral gaits. The latter point is especially important in very large animals because they are inherently less stable (Hildebrand 1985a, 1995). In fact, one way of interpreting this repositioning of the front limbs could be that the condition had evolved specifically to facilitate a lateral gait with long strides, such as the pace— more on this later.

As a final note on the front limbs, it seems somewhat surprising that the scapula of *Arctodus* shows little variation from the typical ursid plan. Even the shape of its vertebral border (an evolutionarily and developmentally plastic trait (Wolffson 1950, Smith and Savage 1956) is essentially of the typical ursid form, and the postscapular fossa housing the powerful subscapularis minor muscle— a trademark of bears— is still prominent in *Arctodus*. This feature and others, such as its plantigrade foot posture (Kurtén 1967a) indicate that *Arctodus* was an incipient, not advanced, courser.

b. Hip and Femur:

Next I discuss hind limb posture and morphology in various carnivores having diverse locomotor abilities and then place *Arctodus* into that spectrum. Many of my quantitative analyses closely follow those of Jenkins and Camazine (1977), and, unless stated otherwise, the data I cite for non-bear taxa comes from these authors. Conformational features I discuss will address the morphology of the pelvis and acetabular joint, along with the shape of the femur and its articulation with the hip. Comparisons will be made in terms of their effects on femoral posture, the limb's line of travel, and locomotor energetics. The carnivores being used for comparison are raccoons, brown bears, felids, and canids. Modern bears and racoons both are amblers which have highly dextrous limbs capable of wide lateral excursions. When they walk their hind limbs circumscribe a broad figure-8 (Jenkins and Camazine 1977) (Fig. 21). Canids contrast most with amblers and other Carnivora in that their limbs are the most restricted in terms of lateral movement (Jenkins and Camazine 1977). In this regard, canids can be considered "strict cursors" because their limbs are essentially useless for most other purposes (besides digging, which in canids has a

motion parallel to running). Felids, on the other hand, use their limbs for many dextrous functions other than locomotion, such as climbing and handling large prey which require more limb mobility (Ewer 1973, Jenkins and Camazine 1977, Kitchener 1991).

The hip and femur morphology of raccoons, classic amblers, gives it a great range of motion in the hind limb, including extensive abduction and adduction. The inferior surface of its pelvis forms a sharp angle when viewed posteriorly (Fig. 22). This angle between the lateral edge of the ischium and the horizontal plane is around 50° in raccoons (Table 10). The acuteness of this angle means that the femur is naturally splayed laterally (abducted). The neck and head of the femur project from the shaft at a relatively obtuse angle — only about 49° — adding further to the femur's naturally abducted position (Table 10, Fig. 22). The femur shaft, however, is bowed inward medio-laterally, which tends to bring the hind foot back to a more medial position under the body, giving raccoons a "bowleggedness" appearance. The acetabulum is shallow and the margins of the articular cartilage are broad. These two features allow for a greater range of rotation of the femur head when articulated. The articular surface of the femur head is quite broad and extends onto the neck, allowing for a broad extent of rotation in the acetabulum (Jenkins and Camazine 1977).

The utility of a mobile femur and hip articulation in raccoons is that it allows the animal to place its legs in almost unlimited postures, which greatly increases stability and maneuverability over broken terrain and during diverse activities. The raccoon commonly scrambles over objects and climbs, necessitating this flexibility. Evidently, there is little evolutionary incentive for racoons to develop structures which limit femur rotation to a parasagittal plane, as these animals have little need to increase locomotor efficiency since they seldom run, nor are they required to maintain significant speeds for long periods or travel long distances. Bear hips resemble those of raccoons in certain ways, but because I want to compare bears more with cursorial carnivores, it will be convenient to first describe hip morphology in the latter.

The canid pelvis and femur (a fox, *Vulpes vulpes*, in the case of Jenkins and Camazine's study) contrast strongly with those of the raccoon, as would be predicted based on the differences in locomotor habits among these Carnivora. The inferior angle of the pelvis is only around 21° in the fox, but my own data show that this angle is considerably steeper in wolves— around 30° (Table 10). The fox's femur neck and head project from the shaft at an angle of approximately 65° (= 53° in wolves) and the femur shaft is rather straight. The net effect of this pelvic angle, the projection of the femur neck, and a straight femur is that the hind limb has little lateral splaying (femoral abduction) compared to raccoons. Because foxes and raccoons are similar in size, it is not appropriate to invoke arguments about body to explain the fox's straighter femur. That is, foxes (and other canids) most likely have evolved straighter femurs to position the leg so that they can swing more in-line with the body and to reduce splaying. The acetabulum in

Table 10. Inferior ischial angle (when viewed posteriorly) and angle that femur neck projects from shaft in carnivores that are discussed in text

species (n)	inferior ischial angle	angle that femur neck projects from shaft	source
raccoon	50°	49°	Jenkins and Camazine (1977)
domestic cat	34	63	Jenkins and Camazine (1977)
red fox	21	65	Jenkins and Camazine (1977)
wolf [1] (10)	30	53	this study
brown bear [1] (6)	62	52	this study
short-faced bear [2] (2)	65	55	this study
spectacled bear (2)	60	n.a.	this study

[1] measured on specimens in the University of Alaska Museum Department of Mammalogy

[2] measured on F:AM 8027 (American Museum of Natural History, New York) and PM 24880 (Field Museum of Natural History, Chicago)

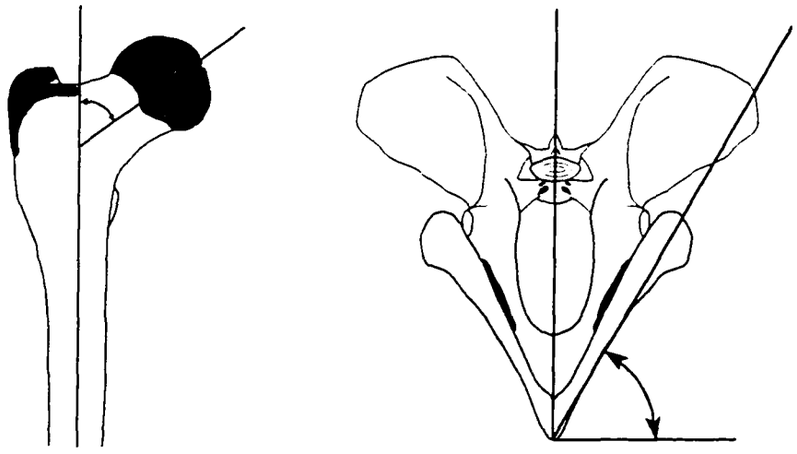


FIGURE 22. Angle of femur neck projection, viewed anteriorly, and inferior ischial angle viewed posteriorly (both examples represent *Arctodus*).

canids is deep and the margins form sharp inward angles, which effectively lock the femur head in place and limit most movement in all but the sagittal plane. The articular surface on the head in canids is the least extensive of the carnivores examined, and it does not extend onto the dorsal neck, being particularly reduced on the medio-ventral margins of the head, which further limits abduction (Jenkins and Camazine 1977). The neck of the femur also is very short in canids.

The femur and hip articulation in canids has the advantage of eliminating the need to control femur position using bulky and energetically costly adductor and abductor muscles. These muscles either have been eliminated, which decreases weight and locomotor effort, or they have been employed as flexors and extensors, which will help distribute the work of locomotion and thus increase endurance (Hildebrand 1995). The effect of these modifications is that canids swing their hind limbs in line with the body more than most carnivores (Jenkins and Camazine 1977). This singular dedication of the limbs must increase efficiency, but it also places limits on dextrous activities. Thus, canids excel at long distance pursuit and prolonged running bouts, but they are for the most part poor climbers and their limbs are nearly useless for grabbing large prey (Ewer 1973).

Felids have evolved quite different locomotor skills and activities than canids, and this is reflected in the morphology of their pelvis and femur. Domestic cats have an inferior ischial angle around 34°, considerably more than foxes, but less than raccoons (Table 10). However, because the neck of the femur projects at 63° (only slightly less than canids), their femur is positioned more vertically, with almost no lateral splaying. And like the fox, there is little lateral flexion of the femur shaft. (When the stance of canids and felids is compared, it can be seen that the canid femur splays outward (laterally) a few degrees, while the felid femur is held nearly perfectly vertical (personal observation).) The acetabular depth is intermediate in cats, with broad coverage of the articular cartilage. In addition, the articular surface of the femur head extends more broadly onto the neck than in canids, but less than in raccoons (data on domestic cats from Jenkins and Camazine (1977)) (Table 10).

These features, characteristic of felids in general, agree well with their habits. Whereas canids have evolved for more or less straight line travel and prolonged endurance, felids are agile, good climbers, and frequently use sharp maneuvers in their predatory tactics. They also use their limbs to handle and subdue prey. These demands require more medio-lateral mobility in the femur, and indeed, the structure of the felid hip articulation facilitates more adduction and abduction than in canids, though not as much as in raccoons. Speed also is vital to felids, and it is important to note that they are quite capable of rotating the femur through a narrow ellipse and in parasagittal plane. However, since felids lack skeletal features to direct this motion, it must require muscular control. In this regard, felids are a compromise morph, and might be said to have "sloppy" limbs because they are not kept in position by skeletal structures so much as by muscles. When felids run, they must be expending energy through adductor and

abductor muscles to keep the legs swinging inclined with the body. This is a costly, but necessary, compromise, since when a lion (for example) catches its prey it must have flexible limbs in order to grab and manipulate the prey (even thought the prey is killed by biting). Often, a lion may even stand on its hind limbs when pulling down large prey. This design probably has placed constraints on felid evolution, in particular preventing them from radiating into niches that necessitate long range, efficient locomotion.

The hips and femurs of bears also reflect a suite of functional compromises, but of a different sort than felids. Bears have pelvises with the steepest inferior angles measured in this (Table 10). Theoretically, this should project the femur laterally at a strong angle. However, the head and neck of the femur typically project from the shaft at approximately 52 ° (in brown bears), which reduces the effective angle of femoral abduction. The acetabulum of bears is more similar to felids, being deeper than in raccoons and shallower than in canids. Furthermore, the articular surface of the femur head is broad in bears and extends onto the dorsal surface of the neck. However, bears are not nearly as extreme in this regard as raccoons.

These characteristics show how the hips of bears, when compared to all other carnivores, have a unique conformation. They resemble other amblers like the raccoon in that their hind limbs are free to move in many planes (but not nearly to the same extent), and their femurs tend to be splayed laterally and then bowed back medially. But bears also are a bit like felids in that the angle of the femur neck increases to compensate for a sharper ischial angle (a sharp ischial angle splays the femur laterally, but a commensurate rise in the neck angle brings the femur back to near-vertical). The ischial angle in bears, however, is extreme, and the angle of the femur neck is not nearly steep enough to bring the femur completely back to vertical. So it seems that bears are doing something quite different in regard to hip conformation. Later, I will show how these features relate best to the ability of bears to use an upright, bipedal stance.

Before bringing short-faced bears into this comparison, I want to examine in detail the position of the fovea capitis femoris (FCF) in various carnivores, using techniques described in Jenkins and Camazine (1977). The FCF, located on the articular surface of the femur head, is the point of insertion for the ligamentum capitis femoris, the ligament directly connecting the femur head to the acetabulum (it originates in the acetabular fossa— see inset of Fig. 23). Since the FCF and the acetabular fossa should be aligned when the femur is positioned neutrally, its placement on the femur head is a good estimator of the femur's natural posture and degree of normal abduction at rest.

The position of the FCF can be quantified for comparison by projecting an equator and a prime meridian on the femur head and then measuring the latitude (E) and longitude (M) of the FCF in degrees (inset of Fig. 23)(Technique of Jenkins and Camazine 1977). In terms of femur posture, M measures the amount of deviation from the sagittal plane, or how much the femur is cocked with the toe inward or

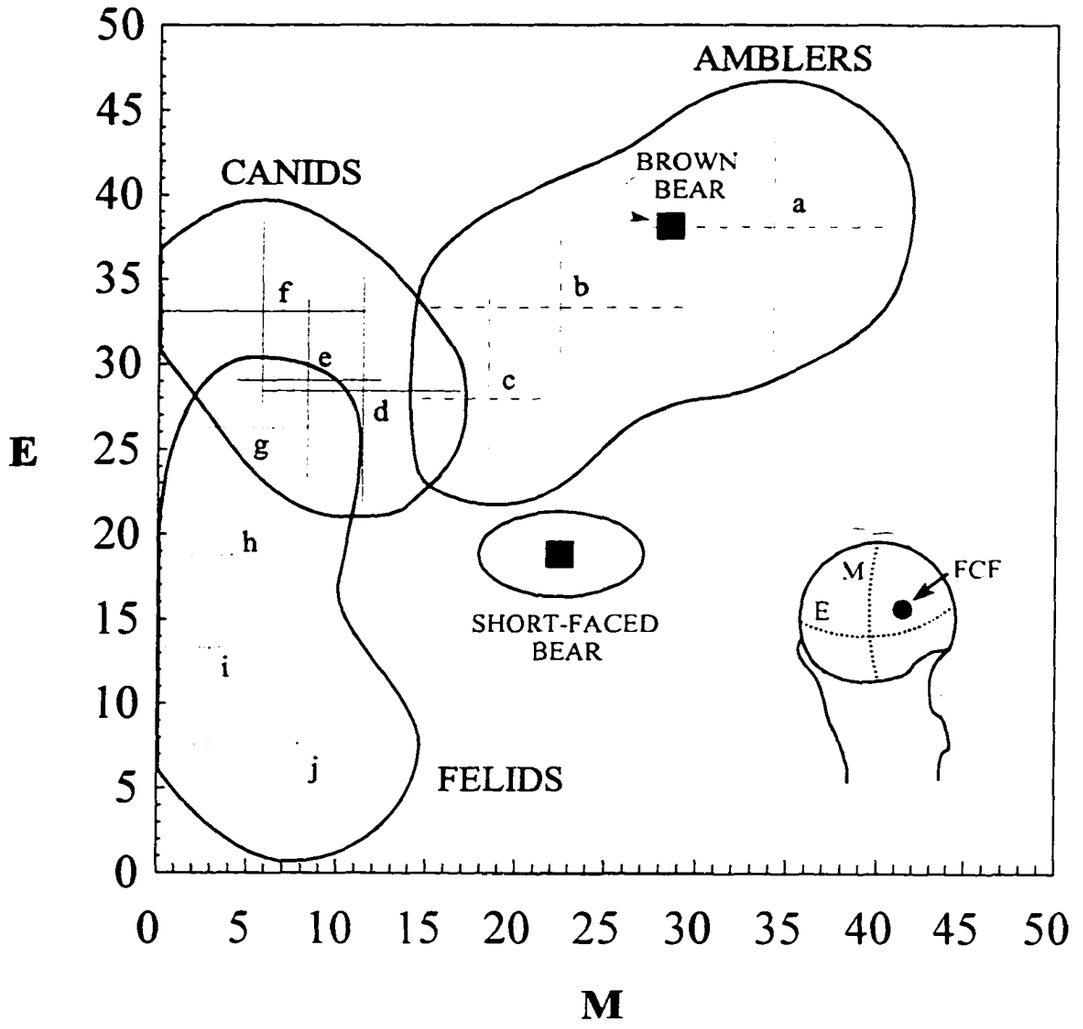


FIGURE 23. Position of the *fovea centralis femoris* (FCF) on the femur head in short-faced bears versus other carnivores. *E* (equator) measures the proximal-distal position of the FCF (in degrees "North") and is an indicator of the extent of femoral abduction when the femur is in a neutral position. *M* (meridian) measures the amount of deviation from the sagittal plane (in degrees "East") and is an indicator of how much the femur is normally chocked outward. Value for short-faced bears was obtained on F:AM 95654, American Museum of Natural History. Techniques for drawing a reference equator and prime meridian are imprecise, so resulting values of *E* and *M* are difficult to reproduce consistently. The ellipse drawn around the value for F:AM 95654 represents a qualitative estimate of its precision. Original graph and data from Jenkins and Camazine (1977, Fig. 9) with data for short-faced bears and brown bears added from this study. (a) bears (*Ursus* spp.), (b) skunks (*Mephitis* spp.), (c) raccoon (*Procyon lotor*), (d) red fox (*Vulpes vulpes*), (e) wolf (*Canis lupus*), (f) African hunting dog (*Lycaon pictus*), (g) puma (*Felis concolor*), (h) bobcat (*Lynx rufus*), (i) lynx (*Lynx canadensis*), (j) cat (*Felis domesticus*).

outward. *E* measures the proximal-distal position of the FCF and indicates the amount of normal femoral abduction. A bivariate plot of *E* and *M* can be used to visually separate animals by their locomotor specializations (Fig 23). These values have been calculated for species of felids, canids, and amblers by Jenkins and Camazine (1977), and are plotted in Fig. 23, along with values calculated for *Arctodus* in this study.

The amblers in Fig. 23, including raccoons, skunks, and Ursine bears, cluster to the upper right, indicative of their highly abducted femurs (*E*) and toe-in stance (*M*). In these regards, Ursine bears appear to stand out as the most extreme, but I would argue that the position of the FCF in bears partially compensates for their strong ischial angles, working in conjunction with an acute angle of the femur neck Nonetheless, Ursine bears cluster well with other amblers.

Felids have both low *E* and low *M* values, meaning their femurs normally have the least amount of abduction and toe-in positioning (i.e., their legs are most naturally inclined with the sagittal plane). This agrees with the observations made earlier and makes sense since felids need to keep their hind legs parallel to the body as much as possible during high speed locomotion. Felids, with their long backs, also have the least problem with front and hind leg interference (described in the previous chapter) so they do not need to swing their hind legs laterally to clear the front legs nearly as much as other carnivores. Also, the pelvis is relatively wide in felids, so the hind legs are naturally positioned farther apart. However, as the previous discussion indicated, felids still retain the ability to move the femur in other planes and its "normal" mode of swinging in the sagittal plane must be maintained by muscular effort.

Canids have *E* values that are much higher than felids, but their *M* values are nearly identical. This is consistent with the typical canid stance where the knees and toes face predominantly forward, in-line with the direction of travel (low *M*), but where the femur is somewhat abducted (high *E*). *E* in canids is on par with amblers, but this should not be taken to mean that actual femoral abduction is equal, since abduction is enhanced in amblers by a high ischial angle. Slight femoral abduction in canids probably reflects their need to swing the hind legs laterally as they move forward in order to avoid interference with the front legs. This compensatory motion must be necessary in canids, in contrast to felids, because canids have relatively short backs and narrow pelvises. Short backs in canids result in a longer period of front limb/hind limb overlap, and narrow pelvises mean that their hind legs are not far apart, which necessitates a slight bow to the legs.

Now I want to examine the hip and femur conformation of *Arctodus* by comparing it to the various modes described for amblers, felids, canids, and other bears. The inferior ischial angle of *Arctodus*' pelvis is high (≈ 65°), but within the range observed for other bears, while higher than its closest relative, the spectacled bear (≈ 60°)(Table 10) (statistical significance has not be determined since the measurement was made on only two *Arctodus* specimens and two spectacled bears). The neck of the

femur projects at approximately 55° from the shaft, slightly higher than in *Ursus*, and commensurate with *Arctodus'* steeper ischial angle. However, the position of the FCF in *Arctodus* is quite divergent from other ursids (Fig. 23), and, in fact, its position is unlike amblers in general.

The low *E* and *M* of *Arctodus* indicate that its femur was less abducted and that short-faced bears required less of a toe-in stance than contemporary bears. In these regards, *Arctodus* had converged on the pattern in felids, having a hind limb that normally assumed a more vertical posture yet retained a high degree of flexibility in multiple planes. Evidence for this flexibility lies in the fact that the acetabulum is not particularly deep in *Arctodus* and that the articular surface of the femur head is fairly broad and extends well onto the dorsal surface of the neck— traits which the norm for bears. The femur and tibia of short-faced bears do not display the bowing seen in other bears, which I think was necessary in part to reduce bending stresses in this huge bear. Recall from the previous chapter that larger animals will reduce curvature in the long bones because it reduces bending moments by keeping the bone more in line with vertical ground forces.

Reduced femoral abduction and less of a toe-in stance mean that *Arctodus* swung its hind limbs in a near parasagittal plane, in-line with the body's long axis. If there was less lateral excursion to the hind limbs, then the feet most likely circumscribed a tight ellipse or figure 8 flight path during each stride. It has been a theme throughout this section that these traits increase locomotion efficiency (and thus endurance and economy of effort), since the legs travel less overall distance per stride, and because more of this distance contributes to forward motion. Furthermore, since these patterns are found universally among cursorial carnivores, their presence in *Arctodus* suggests that this bear was a courser. However, it remains to be explained why *Arctodus* had evolved such an acute ischial angle, compared to its closest relatives, since that promotes abduction. Spectacled bears most closely resemble the primitive stock of Tremarctine bears. The fact that spectacled bears have a less acute ischial angle suggests that there was selective pressure on *Arctodus* to increase ischial steepness. I believe this is where the importance of bipedal standing comes into play.

When a bear stands upright, the femur is severely flexed relative to the pelvis and spine, but it also is highly abducted. Abducting the femur is important when a bear stands up because it provides a wide platform for stability. The extension of the femur head's articular surface onto the dorsal surface of the neck helps facilitates this action, as this is the region that would contact the acetabulum during extreme femoral abduction. Jenkins and Camazine (1977) have documented this trait in the femur heads of brown bears, and I have seen it expressed in brown bears, polar bears, American black bears, and spectacled bears (unpublished data). Since all of these species are able to stand upright, this is not surprising (however, this trait obviously is not unique to bears— see Jenkins and Camazine 1977).

The femur morphology of *Arctodus* is but one line of evidence suggesting that it used an upright

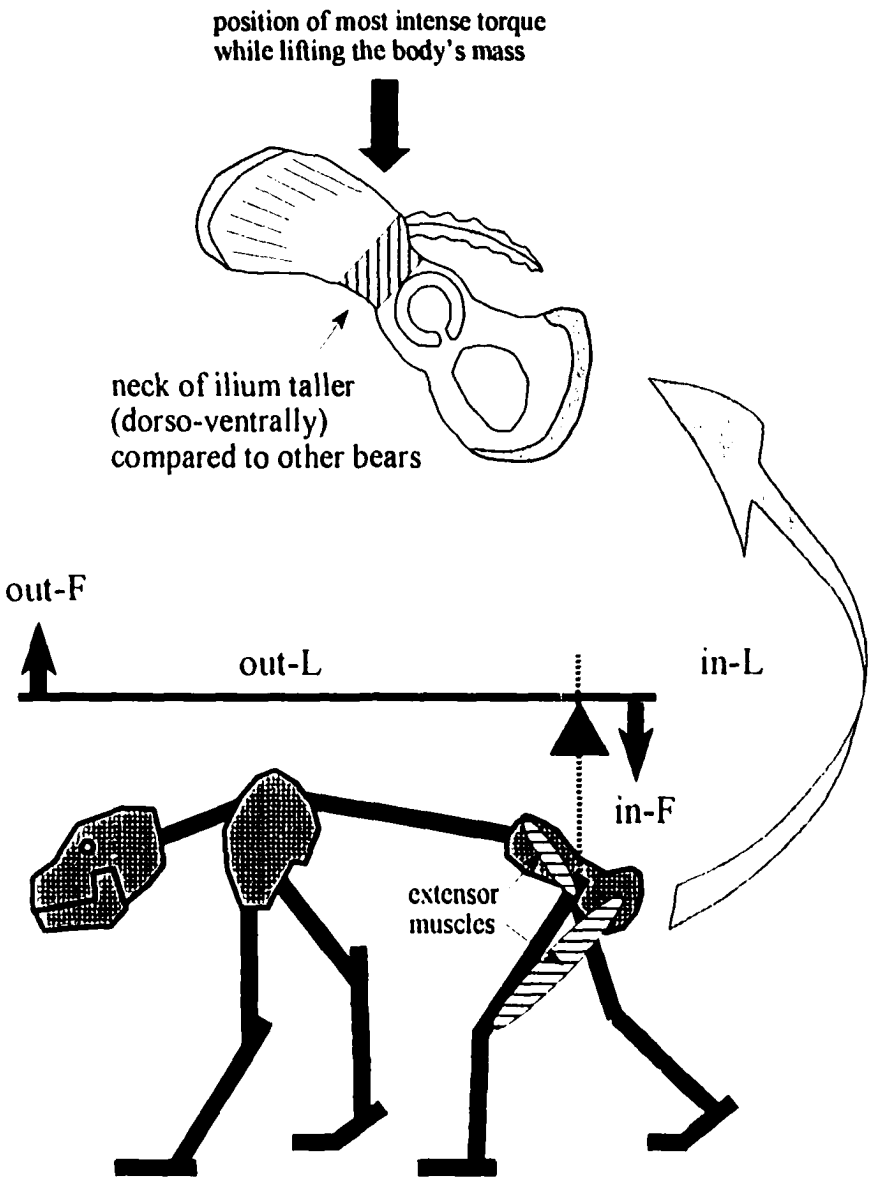
stance. However, additional evidence lies in the morphology of *Arctodus*' ilium and in the length of *Arctodus*' back and hind limbs. The ilium of *Arctodus* has a very wide neck compared to other bears. This has been noted by other authors (Merriam and Stock 1925, Kurtén 1967a, Richards and Turnbull 1996), but its function has remained elusive. I think the function becomes apparent if one considers the mechanics of a bear standing upright. Figure 24 models the mechanics of this action. There, it can be seen that the extensor muscles of the femur provide the force for the action, and the acetabular joint acts as the fulcrum. The inlever of this system is formed by the portion of the pelvis posterior to the acetabulum, namely the ischium. The outlever is formed by the ilium, spine, and head. The torque opposing the lifting action is generated by the entire body mass anterior to the acetabulum. This mass must have been considerable, since it constitutes all of the torso and includes the heavy head. The great length of the outlever relative to the inlever magnifies this torque— all of which comes to bear most intensely at the outlever's proximal end, which is the neck of the ilium.

Three prominent features unique to *Arctodus* (compared to other bears) would have had the effect of improving performance in this lever system (Fig. 24). First, the thick neck of the ilium strengthened the outlever's weakest point in front of the fulcrum. Secondly, the short back of *Arctodus* reduced the length of the outlever, and thus the torque it exerted in resistance against the extensor muscles. Third, the short hind legs of *Arctodus* would have made it more stable during a bipedal stance because its center of mass would have been kept low. Later, I will discuss back length and limb proportions in terms of locomotion, where it will be shown that they confer other advantages. However, none of these traits would have evolved exclusively for one function, and the fact that they increased the ease with which *Arctodus* could have stood upright probably is not insignificant. In the next chapter I will discuss why it seems logical that an upright posture in *Arctodus* would have been advantageous as an aggressive posture for use in intimidating other carnivores at carcasses.

SUMMARY ON CURSORIALISM: I showed that short-faced bears did not lengthen distal limb segments— a trait which might be predicted for a courser— but that this trait is only to be expected amongst advanced cursors because it is beneficial only if the distal segments are light, which they generally are not in bears. Furthermore, long distal segments are most important in cursors that use high speeds, so I suggested that if other cursorial traits could be found in *Arctodus* then this would indicate that it was a cursor that emphasized endurance and locomotor efficiency at *moderate speeds*.

Additional evidence of cursorialism was found. First, patterns of allometry, as well as actual proportions in the long bones, show that *Arctodus* had reduced the overall weight of its limbs. These data also showed that short-faced bears had lightened their limbs distally, but not strongly so. But since gracile limbs are not only lighter, but also weaker, I emphasized that it is unlikely that *Arctodus* engaged in scaled-up, high-force locomotor activities equivalent to other bears.

FIGURE 24. *Arctodus* was configured well for a bipedal stance, which I propose was used as an intimidation posture. It also would have been important for surveying the environment and scenting-out carrion, important traits for a scavenger. The shortened back reduced the length of the outlever (out-L) formed by the anterior portion of the body. This reduced the torque of the body's weight (and heavy head) which opposes the action of the hind leg extensors when a bear stands upright. The neck of the ilium in *Arctodus* was unusually thick and strong compared to other bears. This is the point where the torque of the body's mass is the most intense when a bear stands up because it is immediately in front of the fulcrum in this lever system. Its short hind legs also mean the center of gravity would have been kept low while standing upright.


position of most intense torque
while lifting the body's mass
neck of ilium taller
(dorso-ventrally)
compared to other bears
out-F
out-L
in-L
in-F
extensor
muscles

One of the most prominent signs of cursorialism in *Arctodus* is its advanced limb posture compared to other bears and amblers. *Arctodus*' deep but narrow chest allowed its front limbs to be held more medially beneath the body and facilitated longer strides with less lateral flaring than is typical for bears. The front limbs also were elongated, which further increased stride length and reduced the cost of transport. The configuration of the front limbs conforms with those of cursors that use laterally-supported gaits like the pace. *Arctodus* swung its hind limbs in a near parasagittal plane by reducing femoral abduction and lateral excursions in ways that resemble more cursorial carnivores. However, *Arctodus* retained the ability to abduct the femur when necessary, probably to facilitate an upright stance.

Table 11 summarizes cursorial traits displayed in *Arctodus* and contrasts them with their level of expression in cheetahs (coursers specialized for extremely high speeds) and brown bears (non-coursers). As demonstrated by the patterns in this table, short-faced bears apparently were incipient coursers when they became extinct.

3. Gait Selection and Speed: What Kind of Cursor Was *Arctodus*?

In the previous section, I concluded that *Arctodus* had evolved rudimentary cursorial abilities and that its cursorial adaptations are indicative of a cursor that had evolved to reduce the cost of locomotion at moderate speeds and for sustaining these speeds, rather than for running at high speeds or for other high force activities, such as acceleration or maneuverability— traits necessary for most kinds of predation. Next, I want to analyze other aspects of *Arctodus*' morphology in order to reconstruct its gait and estimate its speed of travel.

Gait Selection

Last chapter, I correlated gait selection in carnivores to proportion in their limbs and back. I noted that a trotting mammal requires a moderate to long back, relative to leg length, so that front-hind limb interference is minimized. Large carnivores with short backs (relative to leg length), namely hyenas and long-legged dog breeds, do not trot but instead use a pace for moderate speed travel. I also contended that the front limbs of pacers (including non-Carnivora) tend to be elongated relative to the hind limbs, giving the back a sloped appearance. Trotting is difficult and inefficient for such an animal because front-hind diagonal pairs of feet cannot take equal-length strides. This is not a problem for pacers where lateral limbs swing as pairs, because flexure in the trunk increases the stride of the shortened hind limbs (this is not possible in the trot because the trunk must be kept stiff). But gait choice is more than just an accommodation for morphology, since gaits also influence energetics. Recall, for instance, that pacers are able to utilize trunk muscles to assist in oscillating the limbs, and pacers can take longer strides than non-

TABLE 11. General cursorial traits and their level of expression in a non-cursor (brown bear), a long distance cursor (short-faced bear), and a high speed sprinting cursor (cheetah).

	cursorial trait	brown bear	short-faced bear	cheetah
degree of cursorial specialization ↓	proximal muscle attachments	no	yes?	yes
	limbs placed medially under body	no	yes	yes
	limbs swing in parasagital plane	no	yes	yes
	distal segments lightened (limb bones reduced, restructured)	no	slightly	yes
	distal segments relatively elongated	no	no	yes
	non-locomotor functions of limbs curtailed	no	no	yes
	digitegrade / unguligrade	no	no	yes
	distal segments lightened further through bone fusion and/or loss	no	no	no

pacers because there is no front-hind limb interference. Long strides correlate directly to a decrease in the cost of transport (Chapter 2, Kram and Taylor 1990). Because of the association between limb morphology, gait selection, and energetics, it seems reasonable to assume that limbs and gaits evolve under strong forces of selection.

To quantify limb and back proportions and assess gaits in *Arctodus*, I will use the Intermembral Index (IMI) and a Back Length Index (BLI) discussed earlier. These indices were calculated for the short-faced bear, brown bear, black bear, polar bear, spectacled bear, wolf, lion, and spotted hyena. These last three (non-ursid) species were analyzed because they represent a broad spectrum of locomotor styles in large carnivores. Modern bears were examined in order to investigate conformational similarities between them and *Arctodus*, which will help determine if they are appropriate analogs for reconstructing gaits in *Arctodus*.[3] The morphology and scaled proportions of these carnivores are compared in Figs. 4 and 5 (Chapter 2).

Calculations of BLI and IMI show that 1) *Arctodus*' back was shorter (relative to limb length) than any of the modern carnivores tested, and 2) the disparity between front and hind limb length was considerable in *Arctodus*', being nearly as great as in spotted hyenas— known pacers (Table 9, Fig. 20).[4] In fact, short-faced bears resemble spotted hyenas more than they do any other carnivore, including other bears, in terms of limb and back conformation. As noted, nearly all large mammals with short hind limbs and tall fore limbs relative to the length of their backs (i.e., tall shoulders) do not trot, but pace when traveling at low to moderate speeds. I conclude from the above data that *Arctodus* would have been a pacer, and perhaps locomoted in other ways similar to spotted hyenas. (After estimating speed of travel below, I will return to a detailed comparison with hyenas).

Acceleration

The IMI also can be used to assess some aspects of a carnivore's ability to accelerate. In the last chapter, I discussed how long limbs in general are not beneficial for acceleration. However, while the best accelerators tend to have short limbs, their hind limbs are long relative to their front limbs (Gonyea 1976). This is characteristic of felids, for example— the best accelerators among large carnivores (Ewer 1973, Gonyea 1976, Kitchener 1991). Relatively long hind legs in felids allow them to burst up to top speeds almost instantaneously because their first stride off the hind legs is essentially a leap from a crouched stance. The crouched stance greatly increases the length of the first stride, which gives the muscles of the

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[3] Complete skeletons were measured for all bears and wolves, including length of individual vertebrae. Data for lions and hyenas were taken from scale drawings and photographs. The validity of this technique was confirmed by performing it on photos/drawings of bears and wolves, for which the actual values were known.

[4] Indices for bears were derived from data in Table 8.

hind limbs a longer contraction period to generate their force (thus, they generate more power). This "leap"allows the limbs to reach a high velocity on the first stride (Biewener 1983b). In contrast to felids, short-faced bears had very short hind limbs relative to their front limbs (high IMI), a configuration that would have greatly reduced their ability to accelerate rapidly (Fig. 20). Likewise, it is reasonable to conclude that *Arctodus* had to take numerous strides to reach top speed.

A relatively long, flexible back, represented by a high BLI, also increases a quadruped's ability to accelerate because it allows the body to be flexed and extended during aerial phases, which increases stride length. Not surprisingly, felids have essentially the highest BLIs of the carnivores tested. The BLI of the polar bear appears to be higher, but this may likely be an artefact of small sample size; bears in general have low BLIs and are too large to flex and extend the back much while galloping. Flexing and extending the back during the aerial phase of a full gallop exposes the spine to sudden vertical forces upon landing, and since the forces of running increase with mass faster than skeletal strength, very large mammals (around 200 kg and above) do not run with flexed backs (Hildebrand 1960). This is not a liability for a large mammal that is able to sacrifice acceleration, and in fact, a stiff back seems to be preferred by mammals of all sizes which engage in prolonged travel. The long distance trotting wolf maintains a rigid back, as do the migrating bison and wildebeest, although for different reasons (Guthrie 1990).

The intermediate back length of wolves (Fig. 20) seems well-suited for an efficient trot because the back is long enough to prevent too much interference between front and hind feet, yet short enough to remain rigid without much muscular exertion. For a trotting wolf (or dog of comparable size), the whole body is noticeably non-compliant and a stiff back provides a rigid platform from which it can suspend its legs (personal observation). In the last Chapter, I showed that non-compliant gaits are more efficient than compliant gaits, and indeed, a wolf can keep up its trot for long periods without fatiguing (Mech 1970). In fact, efficient, long-range trotting could be considered one of the hallmarks of large canid evolution (Ewer 1973). The lion's long back, in contrast, forms a very long span (Fig. 20), which must be energetically more costly to support. Pennycuick (1979) suggested that large felids are generally less efficient at locomotion, compared to other carnivores, because of the dual function of their limbs and their specialization for ambush hunting. While the lion's long, flexible back may detract from locomotor efficiency, these traits enhance acceleration and top speed because they increase stride length during a gallop (Hildebrand 1960, 1985).

Guthrie (1990a) assessed the relationship between back/limb morphology and cantering gaits in wildebeest and plains bison. Guthrie showed that these migratory ungulates need stiff backs to oppose the tension of stretch tendons in their necks in a complex arrangement whereby elastic strain energy is used to "kick-out" the hind legs as the head is lowered. Their back also needs to be stiff because these cantering

ungulates take long strides with their front legs, during which the hind legs are suspended, thereby placing a heavy load on the spine for extended periods (Guthrie 1990a).

Given its size, a flexible and long back would have been fairly useless in short-faced bears. By all modern standards, *Arctodus* was too big to incorporate prolonged aerial phases in its gallop when the back was flexed and extended. The role of the back during locomotion in *Arctodus*, I believe, was somewhat on line with that of large ungulates in that it was involved in the transfer of elastic strain energy. But an even better parallel is found amongst spotted hyenas, so I turn next to a discussion of locomotion in this carnivore, which may appear to have a strange build and unseemly gait, but which in fact is magnificently balanced for an unusual, but effective, form of locomotion.

The Hyena Analogy

In this discussion, I will not be arguing that *Arctodus* was a scaled-up hyena— it was not. Instead, I will show why an animal might evolve some proportions seen in both hyenas and *Arctodus* by discussing the advantages and disadvantages they confer. I begin with a relevant review of the way hyenas approach their prey using different gaits. These generalizations follow patterns established in Kruuk and Turner (1967), Kruuk (1972), and Mills (1989) and from my own observations of videotaped hyenas.

Hyenas are social carnivores, but even when part of a group, each hyena acts and hunts fairly independently or perhaps in pairs, except when specifically hunting for very large prey such as zebra (but even here there is minimal co-ordination of hunting effort). Essentially, each hyena in a "group" is hunting on its own and a pursuit most often is initiated by a single hyena with others apparently joining in when the hunt looks promising. Hyenas seem to test their prey more than almost any other large predator, and it is typical to see an individual hyena move into a group of wildebeest (their primary prey in most regions) and force them to scatter, whereby the hyena can detect or create an opportunity which it can exploit. When such an opportunity arises— for instance the discovery of a wildebeest running awkwardly— other hyenas may join the pursuit or kill.

When hunting in this manner, a hyena use three distinct gaits for different stages of the process. When approaching and scouting a group of wildebeest, the hyena will walk using a long-strided pace. When it confronts and disrupts a group, the hyena will use a faster, bouncy canter (slow gallop) as it assess individual prey for vulnerabilities. If an animal is picked out for pursuit by the hyena, it accelerates from a canter to a full gallop and will pursue intently for usually less than 1 km. At this point, other hyenas may join in.

Kruuk (1972) specifically notes that hyenas often pursue and catch their prey at remarkably slow speeds— often around 15 km/hr. This is because their strategy of moving amongst the herds and constantly testing individuals frequently leads to serendipitous opportunities to kill prey. But it is

important to note that hyenas still rely on high speed pursuit for a large amount of their hunting, and successful hunts at slow speeds are most common during group hunts after zebra. Therefore, it is not appropriate to extend this argument and suggest that short-faced bears could have been successful predators without high speed pursuit. All predators need high speeds, or at least rapid acceleration, at times and must be able to maneuver at those speeds. Plus there is no sound basis to argue that *Arctodus* was social (I believe that the only way a carnivore the size of *Arctodus* could be predatory would be if it used social hunting tactics, but calculations in the next chapter show that a "pack" of short-faced bears would require more prey biomass production than any terrestrial system could provide.)

In addition to the above course of events, five relevant patterns in hyena locomotion are: 1) hyenas continuously change speeds within their gallop (Kruuk 1972). 2) hyenas locomote over a wide range of speeds without changing gait (personal observation). 3) hyenas are on the move and work their prey for longer periods than most predators (Kruuk 1972, Mills 1989). 4) hyenas use a pace for moderate speed travel when scouting an area or moving from one point to another (Kruuk 1972, Mills 1989), and 5) in the Serengeti, hyenas regularly "commute" long distances (~ 50 km) during the dry season to hunt migratory prey (Kruuk 1966, Hofer and East 1993a).

I propose that the key to understanding locomotor strategies and gait selection in hyenas lies in understanding the role of their long necks and heavy heads. Both of these traits are related to the hyena's ability to process large mammal carcasses quickly and thoroughly, and they probably have evolved for these purposes. Part of my contention will be that hyena locomotion and post-cranial morphology have evolved around these constraints.

The heads of hyenas are robust and heavily built to house strong masticatory muscles, massive teeth, and to be able to handle the stresses of forceful biting, including bone processing (Sutcliffe 1970, Kruuk 1972, Ewer 1973). The long, strong neck seems to relate most to competition at kills. Competition between individual hyenas at a kill is keen, and the strategy which seems to have evolved is one where each hyena grabs what it can and eats as quickly as possible before the carcass is totally consumed by other hyenas (Kruuk 1972, Bertram 1979). For this reason, hyenas bolt large chunks of food, but they also remove large pieces— often entire limbs— and carry them a few meters away from the kill, especially when being chased by another hyena (Kruuk 1972). Doing so requires a strong neck since the piece being carried can weigh nearly as much as the hyena itself. For these muscles to evolve such strength, they would have had to become not only wider, but also longer— as per discussions in the last chapter, muscles need to contract over greater lengths to be strong.

To balance this long, heavy neck and head and to prevent their center of gravity from being too far forward, hyenas would have needed to evolve certain modifications to their postcranial morphology. I suggest that the long front limbs and short hind limbs accomplish this by creating a radical pivot point at

the shoulders. If one models the shoulder as a fulcrum with the axial skeleton on the anterior and posterior sides forming two levers, it can be seen the low, heavy hind end has the effect of counterbalancing and passively lifting the heavy head and neck. If the hind end were tall and proportioned like other carnivores, then the hyena's center of balance would be too far forward, and it would be difficult (or at least costly) to keep the head up. Therefore, within this theory, hyenas have evolved short hind ends to mechanically counterbalance the head and keep it propped up.

Next, consider the situation when a hyena scouts a wildebeest herd using a pacing gait. Its head typically is held low (Kruuk 1972), which functions to tense the muscles and tendons of the neck and back, which in turn makes the back more horizontal and elevates the pelvis. This process increases clearance for the hind limbs and allows them to be swung more stiffly (without being flexed), which effectively increases their length and stride. Only when this is accomplished through lowering the head can one front and one hind limb be swung as a pair (pacing). This being achieved, the hyena can utilize a long-strided, efficient pace which allows it to scout herds for long periods without fatigue. Hyenas spend most of their hunting time engaged in this scouting behavior (Kruuk 1972, Mills 1989), and they commonly commute distances of 30 - 60 km between dens and hunting areas (data reviewed by Hofer and East 1993b; also see Pennycuick 1979). Therefore, hyenas represent an example where pacing has evolved in a species where selection should be high for increased locomotor efficiency.

When breaking into a canter and entering a herd, a hyena has a totally different look, not only because of its slow galloping motion, but because its head is raised. Referring back to the lever analogy, raising the head has the effect of releasing tension on the muscles and tendons of the back and lowering the hind end. Since the two hind and two front limbs each swing as couplets independent from each other during the canter, the stride lengths of each couplet do not need to match. Moreover, because the two hind limbs are moving together, they can be swung in a wide arc beneath the body. During this action, the back half of the body essentially moves as a unit, pivoting at the shoulder. When the back legs are then extended, they can make a long stride which propels the animal forward and slightly upward upon which it lands on semi-stiff front limbs. Because the front limbs are not very compliant, but act more as pivot points, the slow gallop has a bouncy, rocking motion. The gait also looks bouncy because the head bobs up and down to alternately tense and relax the back when the hind end flexes and extends. When used at high speeds, the rocking motion decreases because the front limbs flex (become compliant) and increase their propulsive contribution to the gait, rather than just acting as pivot points. During this style of fast galloping, the hind limbs still extend far forward and have an elongated step length because the back flexes considerably. In conventional gallops, the front limbs provide about 65 % of the propulsion (Manter 1938, Cavagna *et al.* 1977), but I would venture that the hind limbs are more important in the fast running hyena.

I also contend that the whole phenomenon of short, sloping backs has evolved in other mammals for the same reasons it did in hyenas— to accommodate a heavy front end. The same pattern can be found, for example, in giraffes and camels, whose long necks would act to amplify the mechanical leverage of the head's weight. Balancing this weight requires getting the back end low to the ground, which is accomplished through a rearward sloping back and elevated shoulders. It seems logical that this was driving body proportions and locomotion in *Arctodus* as well. While *Arctodus*' neck was relatively short (Table 8), its head was very massive (Kurtén 1967a), and either a long neck or a heavy head will place a mechanical encumbrance on the lever system I just described, requiring counter-balancing by the rear-end. Moreover, hyenas, giraffes, camels— and almost certainly short-faced bears— accommodate this morphology by using a pacing gait instead of a trot for moderate-speed travel. As a rough equivalent to trotting, pacing is a fairly fast gait, being quicker than the singlefoot walk (Hildebrand 1976, 1985). It can even be used as a running gait, and I showed that pacers are pre-adapted for efficient, long range locomotion (although non-pacers also may develop this trait). Furthermore, I will show below that because of is size, *Arctodus* would have been a fast pacer.

But is it realistic to extend the hyena analogy so far as to say that *Arctodus* and spotted hyenas galloped in similar ways? I think the answer is yes, to a limited degree. Mechanically, *Arctodus*' gallop must have looked like a hyena's gallop in that the hind end likely moved as a single unit, rocking at the shoulders, and being swung far forward beneath the tall front legs. In application, its likely these two species differed. The hyena's behavior of changing speeds within its gallop allows the animal to break into faster speeds more quickly, which is useful for hyenas in their special form of predation. However, this is not energetically efficient. If my arguments are correct that *Arctodus* would not have engaged in high speed, high force locomotion, then there would be little reason for it to use a variable-speed gallop like that of hyenas. But by no means am I arguing that *Arctodus* could not run. In fact, it may have been capable of fairly high speeds— faster than a grizzly I would think. My argument simply has been that it would have been straight-line running, and a short-faced bear would have needed to take numerous strides to reach top speeds— very much unlike a grizzly. Next, I will attempt a more precise estimation of *Arctodus*' pacing and running speeds.

Speed of Travel

In the previous chapter, I mentioned that there were a number of techniques and formulae available for estimating speeds (but not necessarily top speeds) in extinct animals. Many of these were developed specifically for applications to fossilized trackways left by these animals. These techniques provide general estimates of the speed of travel when the tracks were laid down, but say little about top speeds or normal speeds of travel. Other techniques involve linear correlations between body mass or limb

length and running speed, but these techniques were shown to be very imprecise, especially when applied to very large mammals. Moreover, these techniques have been applied mostly to dinosaurs and provide only very basic estimates of speeds for a group of animals which are essentially a mystery. However, *Arctodus* is essentially a modern mammal with close living relatives, so a more precise indicator of speed should be used. The two methods which seem most applicable are: 1) Alexander and Jayes' (1983) method for scaling locomotion using Froude numbers and linear dimensions, and 2) Garland's polynomial for maximum running speed (MRS) using body mass.

Alexander and Jayes' (1983) method scales locomotion in animals with similar builds but different size using Froude numbers— non-dimensional constants that scale size and motion in dynamic systems. Scaled animals move in dynamically similar ways at speeds that make their Froude numbers equal. Consequently, this method predicts the speed of animals during physiologically-equivalent events, such as the speed of a gait change, using the following equation:

$$F = v^2 / g \cdot l \qquad (20)$$

where F is the Froude number, v is ground speed, g is the force of gravity, and l is leg length (l could also be some other linear dimension of locomotion). Alexander and Jayes have shown further that quadrupeds generally change from a walk to a trot (or pace) at F = 0.5, and from a trot (or pace) to a gallop at F = 2.5 (these are approximate values and the generalization is somewhat oversimplified, but these are the most appropriate values to use for calculation performed below— see Alexander and Jayes (1983) for more detailed correlations between gait change and Froude number).

By scaling limb length (l) in *Arctodus* to that of hyenas, it would be possible to make a fairly accurate estimate of the speed at which *Arctodus* changed from a walking singlefoot to a pace and the speed at which it broke into a gallop. Unfortunately, these speeds have not been measured in hyenas. Nonetheless, it is possible to make rough calculations for *Arctodus* using its limb length and the above mentioned average Froude numbers. Then these estimates can be qualified from observations of how hyenas deviate from other large mammals. Using Formula 20 and values on *Arctodus*' hind limb length in Table 8, I derived the following estimates:

$$speed_{walk\text{-}pace\ transition} = \sqrt{0.5 \times 1.129 \times 9.8\ m/sec} = 2.35\ m/sec\ (8.46\ km/h,\ 5.26\ mph)$$

$$speed_{pace\text{-}gallop\ transition} = \sqrt{2.5 \times 1.129 \times 9.8\ m/sec} = 5.26\ m/sec\ (18.94\ km/h,\ 11.8\ mph)$$

These calculations suggest that *Arctodus* would not have broken into a gallop until reaching

nearly 12 mph, a fairly high speed. Garland's (1983) polynomial formula[5] relating MRS to body mass predicts a top speed of 51 km/hr (32 mph) in a short-faced bear weighing 700 kg (Table 12)(see Fig. 10 of previous chapter and its discussion of Garland's polynomial). But I showed that few mammals actually run with MRS similar to this theoretical prediction, and an animal's build must be assessed qualitatively in order to understand why its actual MRS falls above or below predicted values (Fig. 10, previous chapter). For instance, actual MRS in brown bears is about 40 km/h (25 mph), but Garland's polynomial predicts 55 km/h (34 mph) for a 300 kg brown bear. This and other values in Table 12 indicate that all modern bears have actual MRSs well below speeds predicted from their mass, while obligate predators have MRSs much higher than predicted.

Based purely on the kinematic implications of *Arctodus*' build (i.e., its reduced limb mass), one could conceivably argue that its morphology had evolved to increase top speeds relative to other bears. This essentially was Kurtén's contention, but I have been trying to show throughout these chapters that such an argument is unrealistic: because of its extreme mass, such high speeds most likely would have exceeded *Arctodus*' skeletal strength— at least if it tried to maneuver at these speeds. Without the ability to maneuver, high speeds are of limited value to a predator that hunts solitarily. Given these considerations, a reasonable estimate of MRS in *Arctodus* might be closer to 40 - 45 km/h, rather than the value of 51 km/h predicted by Garland's formula.

Interestingly, the above calculations using Froude numbers indicate that *Arctodus*' moderate speed gait — its pace— would have been fairly fast. In Fig. 8 of the previous chapter, it was shown that mammals normally (and optimally) trot or pace at a speed roughly halfway between their walk-pace transition and their pace-gallop transition. In *Arctodus* this would be about 13.7 km/h (8.5 mph). That is a fairly high value for moderate speed travel, but it does not seem out of line. Mills (1989), for instance, reports that spotted hyenas typically travel cross country at approximately 10 km/h (6.2 mph).

I have argued that short-faced bears were not built specifically to be runners, but I am not contending that they were incapable of running, or never encountered occasions where it was necessary to run. Moreover, my estimates of top running speeds up to 40 - 45 km/hr mean that short-faced bears were not slow. In the next chapter, I explain how competition between Pleistocene carnivores for control over carcasses would have been intense, and why it seems likely that *Arctodus* had evolved to dominate this rivalry. Given this assumption, it is likely that any carcass on the Pleistocene landscape would have attracted quite a bit of attention and would have led to direct conflict among carnivores. In such a situation, short-faced bears would have needed to express their dominance through aggressive behavior and intimidation. As I alluded to earlier, standing upright would have been one likely means to

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[5] $\log MRS = 1.47832 - 0.25892 (\log Mass\text{-}kg) - 0.06237 (\log Mass\text{-}kg)^2$

TABLE 12. Maximum Running Speeds (MRS) in km/h for selected large mammals reported by Garland (1983) versus MRS calculated using his formula: *log MRS = 1.47832 + 0.25892 (log Mass) - 0.06237 (log Mass)*^{2}

species	mass[1]	MRS reported[2]	MRS calculated
CARNIVORA			
Lycaon pictus	20	70	51
Canis familiaris	25	67	52
Canis lupus	40	64	54
Acinonyx jubatus	55	110	55
Panthera pardus	60	60	55
Crocuta crocuta	65	65	55
Ursus americanus	135	48	56
Panthera leo	150	59	56
Panthera tigris	230	56	55
Ursus arctos	300	48	55
Ursus maritimus	400	40	54
Arctodus simus	**700**	—	**51**
NON-CARNIVORA			
Antilocapra americana	50	100	55
Rangifer tarandus	120	80	56
Ovis canadensis	150	48	56
Equus hemionus	260	70	55
Equus zebra	300	64	55
Equus caballis	400	70	54
Cervus elaphus	300	72	55
Alces alces	450	56	53
Camelus dromedarius	500	32	53
Bison bison	900	56	50
Loxodonta africana	6000	35	37

[1] Masses represent species averages reported by Garland, which he collected from various general sources. Therefore, values for mass and MRS not from the same individual

[2] Speeds are those given by Garland. It is well known that many reported top speeds for mammals are unreliable (usually too high), and many of them in this table are undoubtably inaccurate. Despite this, they still represent the values used by biologists because they are the best or only ones available.

accomplish this, but it also is likely that *Arctodus* would have needed to drive carnivores off of carcasses at times, in which case it could have used its modest gallop. *Arctodus* also may not have successfully dominated every situation because some of its rivals were social, and would have aggregated into formidable groups (see next chapter). In these cases, *Arctodus* actually would have needed to run away from a carcass and recalcitrant pursuers. Neither of these types of running (aggressive and defensive) require rapid acceleration or even very high speeds, nor do they demand much maneuverability in the form of sharp turns. These activities seem to be quite within the range of *Arctodus'* structural capacities.

Furthermore, I stated from the onset that it is unrealistic to think that *Arctodus* never would have killed its food directly. I simply am arguing that predatory skills did not form the basis for selection in *Arctodus'* evolution. Even though it seems to have evolved specifically as an exploiter of scavenging opportunities, *Arctodus* undoubtably killed prey that presented itself as an easy target. At times, this would have required a galloping form of running. Finally, although it is speculative, I can imagine a short-faced bear harassing its competitors at a carcass by patrolling around them, demonstrating its presence with a type of bouncing slow gallop similar to hyenas. In fact, this very behavior can be observed today in hyenas which are vigilant in trying to drive lions off of carcasses.

4. Postlogue and Preview of the Next Chapter

At the beginning of this chapter, I stated that there were three credible foraging hypotheses which could explain *Arctodus'* carnivory: 1) it was a powerful predator that overwhelmed very large but slow megafauna, 2) it was a fast cursorial pursuit predator, or 3) it was a scavenging specialist. Each of these hypotheses makes specific predictions about the morphological adaptations one would expect to find in such a carnivore, since each implies selective pressure for very disparate locomotor and dextrous abilities. I have tried to show that the morphology of *Arctodus* does not support the predictions of the two predatory hypotheses, but agrees with those of the scavenging hypothesis. Foremost, *Arctodus'* skeleton was too weak to handle the locomotor forces normally incurred by predators, and indeed, no predator today comes close to *Arctodus'* size. The reason for this is because the relative strength of bone decreases with body size, as does running ability.

In *a priori* evolutionary terms, it is difficult to understand how selection under a predatory lifestyle would lead to the suite of morphological traits found in *Arctodus*. For instance, if *Arctodus* preyed on large, slow-moving pachyderms (hypothesis 1), then why did it evolve such a gracile build? It would seem that such a predator would need to be as strong as possible and built more like a typical bear. If *Arctodus* preyed on fast prey (hypothesis 2), then why was it so large and gracile? To capture fast prey,

Arctodus would have evolved in a direction that increased speed, maneuverability, and acceleration. Since smaller carnivores are more adept at these skills than larger ones, selection is predicted to have favored smaller body size in short-faced bears. Even if evolution did lead to a predator the size of *Arctodus* which engaged in high force running (something that I showed was highly improbable), then it most certainly should have evolved a more robust, not more gracile, skeleton.

Although not a fast or agile runner, *Arctodus* was an incipient cursor with features indicating it was built for locomotor efficiency and for sustaining moderate speeds over extended periods using a pacing gait. Stable isotope data indicate that *Arctodus* was carnivorous, so I suggested that these morphological traits would be most advantageous in a scavenger which needed to cover a very large home range. This seemed logical since one might predict that carrion resources were widely scattered and unpredictably distributed during the Pleistocene. A scavenger searching for large mammal carcasses on the landscape would need to cover a large area and stay on the move in order to increase its chances of finding enough carcass biomass to sustain itself.

The next chapter examines the energetic ecology of these predictions and tests them in a model of Pleistocene carcass production. In that chapter, I also discuss the necessary conditions leading to the evolution of a pure scavenging niche in a large carnivore, and I finish by suggesting probable mechanisms underlying *Arctodus*' extinction.

CHAPTER IV

LOCOMOTOR PERFORMANCE AND ECOMORPHOLOGY OF SHORT-FACED BEARS

PART III: FORAGING ENERGETICS, CARCASS PRODUCTION, AND THE EVOLUTION OF *ARCTODUS*' SCAVENGING NICHE [1]

1. INTRODUCTION

In the previous two chapters, I established arguments contending that *Arctodus*' post-cranial morphology had evolved for increased locomotor efficiency within a scavenging niche. This paper explores probable ecological and energetic reasons for the association between locomotor efficiency and scavenging.

Energetic axioms predict that a very large carnivorous endotherm will require a very large home range and that it will not have a high population density (Clutton-Brock and Harvey 1978, 1983; McNab 1963, 1980; Eisenberg 1981). Trophic principles and rules of ecological efficiencies dictate further that terrestrial carnivores have much lower population densities than herbivores and that larger carnivores will have even lower densities (Elton 1927, Slobodkin 1961, McNab 1980, Gittleman and Harvey 1982). As generalities these axioms suggest reasons to hypothesize that a pure carnivore the size of *Arctodus* would have needed to forage over an extremely large home range in order to obtain enough food to meet its energetic requirements.

Consider the case where such an animal also foraged on widely dispersed food items and invested considerable search effort into each unit of food— food units such as large mammal carcasses that are large and widely distributed in space and time. Optimal foraging theory predicts that this "big investment, big reward" system should lead to both larger size and increased locomotor efficiency. Increased size is predicted because a larger animal 1) can eat more at one feeding when it finds a large food item, 2) can go longer between meals, and 3) has a reduced cost of transport. Increased locomotor efficiency is predicted because such an animal should not expend more energy searching for food items than it gains from them (Emlen 1966; Schoener 1969, 1971, Rapport 1971; Pyke *et al.* 1977; Houston 1979; Krebs *et al.* 1981; Eisenberg 1981).

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[1] This chapter was written as the third part of a three-part monograph on the locomotor adaptations and ecomorphology of short-faced bears. Chapters 2 and 3 constitute the other two parts.

These sorts of predictions provide the ecological reasoning to argue that *Arctodus*' morphology would have been most adaptive within a scavenging niche. Without this rationale, it would remain unclear why a carnivore would evolve the morphological traits found in *Arctodus*, including its extremely large size. This reasoning also provides an additional means to test the scavenging hypothesis. Namely, it should be possible to model the energetic needs of a population of scavenging short-faced bears and examine whether Pleistocene ecosystems were capable of supporting these needs. If these ecosystems did not produce enough carrion biomass to support the population, then the scavenging hypothesis can be rejected. In this chapter, I perform this test by modeling energetic and life history parameters of the *Arctodus* population in eastern Beringia, and the likely amount of carrion that Beringia would have been producing.

Throughout this modeling exercise I will rely heavily on established correlations between body size and energetic life history parameters in modern carnivores, but frequently I will draw back from these strictly mathematical correlations and modify them by using direct observations and analogies in modern carnivores. Even though *Arctodus* inhabited a variety of landscapes and ecosystems in North America, I will be constructing input variables based purely on ecosystem parameters in eastern Beringian, to keep the model manageable. This approach also should provide the most rigorous test of the scavenging hypothesis because Beringia was relatively less productive than other Pleistocene ecosystems (Hopkins *et al.* 1982, Guthrie 1990). To construct the model, I will estimate the annual food requirements (kg of meat/km^2/year) of a carnivore the size of *Arctodus* (700 kg), followed by an estimation of individual home range size and population densities so that I can determine the annual carrion requirements (kg/km^2/year) of a minimum viable population of short-faced bears. Then it will be necessary to compare this requirement to the amount of carcass production which could be expected from Beringian ecosystems. To do this, I will estimate carcass biomass production via both predation by large carnivores and natural mortality in Beringia's large herbivores (kg/km^2/year). Both of these latter tasks will require secondary modeling of population dynamics and productivity in both herbivores and carnivores.

2. Forage Requirements and Population Parameters

In order to model the energetic ecology of the entire population of short-faced bears in eastern Beringia, I first will need to estimate the foraging area and annual energy budget of a single bear. Then, after making certain demographic considerations, this budget can be extrapolated to the whole population, whose size also will need to be estimated. Fortunately, numerous studies have documented correlations between body size and a wide range of energetic life history traits in mammals; many of these relationships have been specifically developed for carnivores (summaries in Kleiber 1932, 1961, McNab

1963, 1980, 1983, 1989, 1990; Gittleman 1985, 1986; Damuth 1987; Peters 1983; Calder 1984; Eisenberg 1981; Schmidt-Nielsen 1984).

As with other scaling relationships, these correlations are described in terms of the allometric equation:

$$P = b\,M^{a} \tag{21}$$

where P is the parameter in question and M is body mass. The regular log-linear relationship between various biological parameters and body size is premised on the scaling of metabolic rate to body size in endotherms. Using these empirical relationships, one can cautiously predict general features about a species, such as its home range, foraging (energetic) requirements, and minimum viable population density, based solely on its body mass and trophic level. Many authors warn that such scaling relationships are purely descriptive of the species they are measured in, and are not intended to be used as predictors in unstudied species. However, these relationships provide a good starting point to estimate such variables in an extinct population since they certainly suggest general trends within a group of animals. Naturally, it may be necessary to qualify a prediction based on ancillary information, and I will be doing this throughout the following sections.

Forage Requirements

Harestad and Bunnell (1979) show that the amount of flesh consumed per day by a carnivore (FC in grams) is equal to:

$$FC = 1.7\,M^{0.65 \pm 0.02} \tag{22}$$

(in this equation, M also is in grams). For a large 800 kg male short-faced bear this would be equivalent to 17.6 kg (17561 g) of food eaten every day, or 6424 kg per year. A 600 kg female would require 5271 kg/year, and the population average (assuming 700 kg) would be 5853 kg/year. Farlow (1993) derived an estimate of annual mass-specific food intake for predators as:

$$FC = 48.87\,M^{-0.30} \tag{23}$$

where FC is kg food consumed per kg body mass per year. Using this equation, the annual kg of flesh eaten annually by the average 700 kg short-faced bear would have been 4793 kg, somewhat less than the first estimate.

Harestad and Bunnell's equation is derived from actual values on grams of food consumed per day by mammalian carnivores as reported in field studies, but includes all types of food eaten (i.e., flesh and vegetable matter) and their data were derived mostly from small carnivores. Farlow's equation is more theoretical. First, he uses food consumption rates (in watts) reported for a wide range of birds and mammals, including herbivores. Then he converts watts to kg of flesh required by a carnivore using the energy content of animal tissue (≈ 7,000,000 joules/kg). Farlow's method yields a lower value probably because it unrealistically assumes that all food eaten by a carnivore is pure flesh, which is relatively high in energy content. I am inclined to use Harestad and Bunnell's equation because it is derived from data on actual mammalian carnivores, and its higher prediction of flesh requirements will be a more rigorous test of the scavenging hypothesis.

Furthermore, I tested the predictive ability of Equation 2 using known rates of food consumption in large predators and found it to be quite accurate. For instance, spotted hyenas in the Serengeti consume 3 kg of prey per day, equal to 1095 kg per year (Kruuk 1972). Using a value of approximately 60 kg for the weight of an average Serengeti hyena (Kruuk 1972, Nowak 1991), the equation predicts this consumption rate perfectly. However, as I will discuss later, hyenas in Ngorongoro consume only 2 kg/day. The disparity arises probably for two reasons: 1) the method by which "consumed" prey is calculated (see below), and 2) because hyenas in Serengeti make long "commutes" between denning areas and foraging areas to hunt migratory prey, whereas hyenas in Ngorongoro do not commute (Kruuk 1972, Hofer and East 1993a). Therefore, Serengeti hyenas truly may eat more because they incur greater costs of locomotion.

In comparison, Kolenosky (1972) estimated that wolves (somewhat smaller than hyenas) hunting white-tailed (*Odocoileus virginianus*) deer in Ontario consume 0.1 kg of prey per kg of 1 kg of body mass, which is twice the rate of hyenas. Mech *et al.* (1971) estimated 2.5 kg of deer per day for wolves in Minnesota, which is only slightly greater than the amount predicted for a 40 kg wolf (2.3 kg/day) by Equation 2. Numerous other studies on wolf foraging also have shown that individuals consume about 1.5 - 3.0 kg/day (e.g., Pimlott *et al.* 1969; Mech 1970, 1977; Peterson 1977; Peterson *et al.* 1984; Fritts and Mech 1981; Ballard 1981, 1993; Ballard *et al.* 1987). Field data on consumption rates can only be taken as rough approximations of food requirements because these calculations are made by dividing the estimated prey mass killed by total predator mass. Prey mass almost always is estimated, and the assumption that this entire mass is consumed, or consumed by the predator in question, is seldom valid. Wolves also have been known to consume over 12 kg of food at one feeding (Mech 1970), and Kruuk (1972) recorded one hyena eating 14.5 kg and another eating 9.3 kg in single feeding bouts. Incidences like these can potentially lead to an overestimation of daily food intake and energy requirements.

Carcass Requirements

In order to estimate carrion requirements of a scavenging short-faced bear, consumption data must be converted to carcass biomass. For modeling purposes, I will assume that carrion in the Beringian system was being produced by the hunting activities of large predators and natural mortality in the three dominant large herbivores— mammoth, horse, and bison (Guthrie 1968, 1982, 1984a, 1990a). The following values for herbivore body mass will be used:

mammoth	3800 kg
bison	650 kg
caballine horse	175 kg

These represent an approximation of mean adult body mass averaged for males and females, but they differ from estimates used in other studies, so I will explain their derivation.

Mammoth: The wooly mammoth (*Mammuthus primigenius*) was the smallest species of mammoth. Shoulder height was about 2.8 m according to Kurtén and Anderson (1980), which means it stood a little shorter than the African bush elephant (*Loxodonta africana cyclotis*) and a little taller than the African forest elephant (*Loxodonta africana africana*). Its shoulder height is more on line with the Asiatic elephant, to which it is more closely related (Kurtén and Anderson 1980). Haynes (1991) notes that mammoth limb bones are 20 % wider than *Loxodonta* bones of similar length, meaning mammoths were either engaging in higher stress activities or were carrying more body weight for their height— most likely the latter, since mummies of mammoth show that they carried large amount of fat through the winter (Guthrie 1990). Using this information and the weights listed below from Nowak (1991), I will assign mammoths a weight of 2700 kg for females and 4900 kg for males, with an average of 3800 kg (Table 13). Guthrie (1968) used an estimate of 3000 kg, while Bliss and Richards (1982) (in a model discussed later) used 2230 kg, for unspecified reasons. My estimate is higher because I am interpreting the mammoth's stouter bones as an indication that these proboscideans were more heavily built for their height compared to modern elephants.

Horse: It is now apparent that two size classes of horses probably inhabited Beringia during latter stages of the Pleistocene, a moderate-sized hemione (*Equus (hemionus)* cf. *kiang*) and a smaller caballine (*E. (caballus) lambei*) (Guthrie 1968, 1982, 1990a; Guthrie and Stoker 1990; Sher 1974, 1986, 1987; Harington and Clulow 1973; Harington 1977, 1978, 1980b; Burke and Cinq-Mars 1996). The temporal range and taxonomy of these two equids are unclear but it seems likely at present that they were contemporaneous. However, the fossil record indicates that the smaller caballine may have been more common, so I will use it as the representative equid (biomass representation is balanced by the fact that

TABLE 13. Weights of modern elephants (from Nowak 1991) and estimates of male and female mammoth weights.

	female		male	
	weight- *kg*	shoulder ht.- *cm*	weight- *kg*	shoulder ht.- *cm*
L. africana cyclotis	range 2400 - 3500	240 - 340	range 4000 - 6300	300 - 400
	mean 2800	250	mean 5000	320
L africana africana	range —	160 - 240	range — - 6000	160 - 286
	mean 2700	210	mean —	250
Elaphus maximus (Nowak	range —	250 - 300	range —	250 - 300
makes no distinction for	mean 2720	—	mean 5400	—
male-female shoulder ht.)				
Mammoth primigenius	mean 2700	—	mean 4900	—
	average mammoth = 3800 kg; shoulder ht. = 2.8 m			

the smaller species would have had higher population densities). Modern domestic and feral horses have a considerable size range, often averaging 350 - 500 kg, but some may approach 1000 kg. Their large size in general is a product of domestication. Primitive wild caballines such as the tarpan and Przewalski's horse are smaller and stockier and weigh 200 - 300 kg; Ponies, such as the Shetland are about 150 - 175 kg (Nowak 1991). Since the small caballine of Beringia was, on average, a little larger than a Shetland (Guthrie 1984a), I will assign it a weight of 175 kg. In Guthrie's (1968) biomass estimates, he assigned horses a mass of 250 kg, but this was before it was recognized that two size classes inhabited eastern Beringia. Bliss and Richards (1982) used an estimate of 150 kg in their model.

Bison: To my knowledge, no one has systematically estimated the mass of Pleistocene steppe bison (*Bison priscus*) using skeletal indicators. However, it is widely accepted that they were larger than either present day plains or wood bison (Skinner and Kaisen 1947; Guthrie 1968, 1970, 1990a; Harington 1977, 1978, Kurtén and Anderson 1980, Anderson 1984, McDonald 1981). Data in these studies indicate that steppe bison may have been 15 - 20 % larger than either modern plains (*bison bison bison*) or wood bison (*Bison bison athabascae*). Nowak (1991) listed a size range of 350 - 1000 kg for modern plains bison, with an average weight around 450 kg for females and 750 kg for males. Carbyn *et al.* (1993) estimated the average weight of modern male and female wood bison to be 625 kg and 450 kg, respectively. Adding 15 - 20 % to the average weight of modern bison (= 550 kg, combined for males and females), yields 633 - 660 kg. Considering these data, I will use a weight of 650 kg for *Bison priscus* in this model. Guthrie's (1968) rough approximation for the average weight of steppe bison was 500 kg, and Bliss and Richards (1982) used 450 kg in their model, based on the weight of modern bison (Bliss and Richards did not adjust for Pleistocene body size).

Total Carcasses: In terms of whole carcass mass, 5853 kg (the annual dietary requirement of an average short-faced bear) is equivalent to:

9.0 bison, or
33.4 caballine horses, or
1.5 wooly mammoth

Obviously, certain qualifications to these estimates are in order. First, roughly 10 % of a large mammal's body mass is composed of skeleton, which I will consider to be inedible for now. In terms of edible, caloric portions, about 45 % of body mass is muscle, and the balance is comprised of skin, digestive organs, fat, blood, and liver in descending order (Calder 1984). Considering that the energy content and digestibility of these tissues differs, and accounting for skeletal weight, I will use a value of 75% for the edible and accessible body mass of a whole mammal. This also is the value used by Peterson (1977), while Schaller

(1972) suggests it is lower and Pimlott (1967) estimates 80% (also see Fuller and Keith 1980). With a 75% adjustment, the number of carcasses required annually for one short-faced bear becomes:

12 bison, or
44.6 caballine horses, or
2.0 wooly mammoth

It is just as important to consider that a scavenger will seldom encounter a complete carcass and that carcasses putrefy over time, at a rate that is dependent on temperature. For instance, in subtropical grassland and savannah ecosystems with high densities of competing carnivores, carcasses usually do not last more than a few hours to a few days, depending on their size. Carcasses < 113 kg are completely consumed within 4 hours in the Serengeti and Ngorongoro ecosystems, usually by the predators that killed them (Blumenschine 1987). Adult African buffalo (*Syncerus caffer*; 300 - 900 kg), however, persist for nearly four days on average, and elephants can last 11 days before putrefying if they are not found by carnivores (Blumenschine 1987). These estimates are also in line with Houston (1979).

Carcasses of ungulates in northern North America tend to last longer than similar-sized African species. Ungulate carcasses in Alaska, Minnesota, and northwestern Canada remain on the landscape for about 4 to 5 days in late winter and spring and 2 - 10 days in summer, but they are repeatedly visited and fed upon by carnivores during that time (Magoun 1976, Magoun and Valkenburg 1996, Haynes 1982, Oosenbrug and Carbyn 1982). Here, brown bears, wolves, and wolverines are the main large-bodied carcass consumers. In Wood Buffalo National Park, Alberta, wolves spend an average of 2.5 days on a bison kill in winter before moving on, but they may return to the carcass again later in the season; soft tissue can be found on bison carcasses in the park for up to 1 month, after which only bone remains (Oosenbrug and Carbyn 1982). On Isle Royale, wolves preying on moose utilize nearly the entire carcass over the course of a few days (Mech 1966, 1970).

In Africa, carcasses are processed very rapidly mostly because of intense competition amongst large carnivores, but in North America the competition is less intense and dominance hierarchies are simpler: brown bears dominate over both wolves and wolverines at carcasses unless highly outnumbered. However, brown bears are only competitors in the summer, leaving just wolves and wolverines along with raven and fox in the winter. In Alaska, brown bears and wolverines process and protect carcasses more thoroughly than do wolves, although carcass utilization increases in all three carnivores when carcasses are not abundant, or when these carnivores are denning and feeding young (Murie 1944, 1981; Magoun 1976; Magoun and Valkenburg 1996; Haynes 1982; Gardner 1985).

This information suggests that competition for carcasses would have been a key issue for any

scavenger in Pleistocene North America, when carnivore diversity was higher than at present. But *Arctodus* almost certainly would have been dominant over other Pleistocene carnivores, except perhaps for large groups of social carnivores (Matheus 1994a, 1995, and following chapter), so it would be inaccurate to envision *Arctodus* as being dependent on random carcass availability in the form of "leftovers" from other carnivores. At the end of this paper I evaluate the level of sociality in Pleistocene carnivores and their competitive interactions with *Arctodus*. There I will make the argument that competition for carcasses was indeed keen, and that body size in *Arctodus* most likely was driven by its need to exert dominance. Likewise, body size and the size of social units in other Pleistocene carnivores most likely were shaped by this highly competitive environment.

Population Density and Home Range Size

As a starting point for modeling carcass availability, I first will estimate the population density and home range size (HR) for short-faced bears. In the next section I will calculate the required carcass density for such an area. Both population density and HR size have been scaled to body size in mammals and are tied to the scale effects of metabolism, the density of food energy (productivity) on the landscape, and trophic level (McNab 1963, 1980, 1983; Harestad and Bunnell 1979; Eisenberg 1981; Damuth 1981, 1987). It is important to note that an individual's HR may not translate directly to population density, unless it is an exclusive HR, which is rare (Sandell 1989). In addition, HR can include areas that an animal occupies for reasons other than foraging. Still, it will be instructive to explore predictions for both density and HR in a carnivore the size of *Arctodus*, and then discuss them in terms of other large carnivores.

Harestad and Bunnell (1979) provide the most recent estimate of home range size specifically for carnivores:

$$HR = 0.11\,M^{1.36} \quad (r^2 = 0.81) \tag{24}$$

where mass is in grams and HR is in hectares. Note that the scaling exponent is >1, meaning home range requirements increase faster than body size in carnivores. The exponents for herbivores and omnivores range between < 1 to not significantly different from 1. According to Equation 4, each 700 kg short-faced bear is predicted to have a home range of 9,788,722 ha (97,887 km^2; equivalent to 24,471,805 acres, or 38,237 $miles^2$) — an area nearly as large as the state of Ohio, which is obviously unrealistic. This is a good example of how it does not work well to scale some life history parameters over a large range of body sizes, and why these types of relationships often fail as predictive tools. However, this calculation emphasizes the fact that *Arctodus* would need to forage over an enormous area simply because of its size

and trophic level. Indeed, the positive scaling of foraging area to body size in secondary consumers is the primary reasons why it is believed that carnivores do not attain such large sizes (Elton 1927, Colinvaux 1978, McNab 1980, Eisenberg 1981) and why Emslie and Czaplewski (1985) argued that *Arctodus* could not have been carnivorous.

Turning to density estimates, Damuth (1987) compiled data on population densities in hundreds of terrestrial mammals, including 46 carnivores ranging in size from small mustelids to bears. His regression for population density (D) in "vertebrate-consumers" is:

$$D = 3.47 M^{-0.96} \quad (r^2 = 0.67) \tag{25}$$

Assuming an average weight of 700 kg for *Arctodus* (half males, half females), Damuth's equation predicts a density of 0.0064 bears/km^2, equivalent to 156 km^2 for each bear (134 km^2 for a 600 kg female, and 176 km^2 for an 800 kg male). It is important to note, however, that Damuth's equation is derived almost entirely from carnivores that are predatory. In other words, estimates based on his equation are indirect estimates of prey densities, not carcass densities. Naturally, carcass densities will be much lower than prey densities. Therefore, the calculation of 156 km^2 for each short-faced bear will be regarded as the maximum theoretical density of individuals in prime habitat, but it cannot be construed as an estimate of individual HR size.

Lacking an accurate mathematical predictor of HR or density in such a large scavenger, I will make a some approximations using comparisons to other large, solitary Carnivora. The HR of barren ground grizzlies in arctic Canada, where bear densities are very low, is around 414 km^2 for males and 73 km^2 for females (Pearson 1975, 1976), but values as high as 3029 km^2 have been reported for individual bears (Servheen 1983). Ballard *et al.* (1981) estimated an average HR between 313 - 382 km^2 for grizzlies in southcentral Alaska. Again, these are HR sizes, not population densities. For perspective, the HR predicted for a 200 kg grizzly using Harestad and Bunnell's equation for carnivores is 1,781,531 HA, or 17,815 km^2— again, extremely divergent from any realistic value. But grizzly bears may not be good analogs for HR in short-faced bears, since grizzlies are not strict carnivores. Harestad and Bunnell's equation for HR in omnivores is:

$$HR = 0.059 M^{0.92} \quad (r^2 = .90) \tag{26}$$

For a 200 kg grizzly, Equation 26 predicts 44 km^2 — close to the minimum HR in a female grizzly in some habitats, but it still is a poor estimate for the species' average.

Nowak (1991) lists a wide range of HR values for brown bears, from an average of 80 km^2 in

Yellowstone, to upwards of 600 km^2. Over the course of a lifetime individual brown bears can inhabit an area covering thousands of km^2, and males tend to have much larger HRs. There can be considerable overlap in brown bear HRs, and population densities are on the order of one bear per 100 km^2. In Denali National Park, Alaska, the density is one bear per 30 km^2, while in tundra areas of northern Alaska and Canada it is one bear per 150 km^2 (Nowak 1991).

Data from puma may be instructive since it is a wide-ranging solitary carnivore that lives in low densities. Puma have HRs as large as 277 km^2 according to sources cited in Sandell (1989), and as large as 293 km^2 according to Nowak (1991). But a cougar in Texas was reported to have roamed over 1826 km^2 (Lindzey 1987). Based on data in cumulative sources cited by Nowak (1991), a good approximation for average puma HR seems to be around 150 km^2. Population densities for puma range from 0.048 - 0.005 puma/km^2, or 1 puma every 21 - 200 km^2 (Nowak 1991), so even this solitary, reclusive carnivore may experience considerable overlap in HR (mostly between males and females).

Next, I will discuss data on wolf demographics in a fair amount of detail because the information will be used later when I model population parameters in Pleistocene carnivores.

Harestad and Bunnell (1979) calculated a mean HR size for wolves of 2027 km^2, based on published data. I believe their value is erroneous and represents the HR of entire packs, not individual wolves (this mistake probably is partially responsible for their inaccurate line of allometry correlating HR to body size in very large carnivores). A closer look at specific data shows that individual HRs are much smaller.

Wolf packs in northern Alaska and northwestern Canada typically range over an area around 500 -1000 km^2 through the course of a year, and generally are comprised of 5 - 9 permanent members, equivalent to 56 - 143 km^2 per wolf (Murie 1944; Mech 1970; Ballard 1982; Ballard *et al.* 1981, 1990; Stephenson and James 1982; ADFG Wolf Report 1994). Wolves hunting bison in Wood Bison National Park, however, form packs averaging around 10 individuals (Oosenbrug and Carbyn 1982). Stephenson and James (1982) report that wolf densities in northwestern Alaska are around 0.0026 wolves/km^2 in the foothills of the Brooks Range, but down around 0.0019 wolves/km^2 on the Arctic Slope. The later value is the same reported by Nowak (1991) for the lowest known density of wolves. Home ranges are large in northwestern Alaska, around 1300 km^2 for packs of about 5- 8 individuals. Ballard (1993) found local areas in this region with wolf densities ten times as great in prime habitat, but area-wide densities are on the order of 0.004 wolves/km^2 according to estimates by the Alaska Department of Fish and Game (ADFG Wolf Report 1994). Statewide estimates from this report show that overall wolf densities in northern Alaska are generally between 0.002 - 0.005 wolves/km^2, pack size is around 5 - 9 wolves, and HR size for an average pack commonly reaches 1000 - 2000 km^2.

In southcentral Alaska, Ballard (1982) reports that the 61,595 km^2 Nelchina basin supported

approximately 450 individuals in 1965. This is equivalent to 0.007 wolves/km^2 (137 km^2 per individual wolf). However, a fair amount of this area— about 18,798 km^2— is high altitude, and Ballard implies that this area is not part of normal wolf habitat. Adjusted density in the Nelchina basin using the 1965 population then would be 0.011 wolves/km^2 (95 km^2 per wolf). This agrees with Ballard's estimate of 73 - 119 wolves per km^2 during the mid-1970s. Since this population was recovering from a previous predator control project, it was nowhere near carrying capacity in 1965. Home range size in these packs was on the order of 500 - 800 km^2, and an average pack had around 8 individuals. The ADFG 1994 Wolf Report indicates that densities of wolves in interior and southcentral Alaska generally are around 0.005 - 0.01 wolves/km^2, pack size is around 6 - 9, and pack HRs are on the order of 600 - 1000 km^2. Pack size tends to be larger for wolves that hunt large prey like moose (Earle 1987).

Home ranges for wolves in the southern part of their North American distribution are smaller and their densities are considerably higher than in the north. In Algonquin National Park (Ontario), where wolves feed mainly on white-tailed deer, packs of 4 - 7 wolves typically have a HR around 100 - 300 km^2, or approximately 35 - 40 km^2 per wolf. Overall densities in Algonquin are 0.038 wolves/km^2 (Pimlott *et al.* 1969). In northern Minnesota, wolves also primarily hunt white-tailed deer, but their HR size tends to be larger— around 200 -350 km^2 for a pack of 5 - 8 wolves, or around 50 km^2 per wolf. Average densities there are approximately 0.015 - 0.040 (Mech 1970, Van Ballenberghe *et al.* 1975, Fritts and Mech 1981, Nelson and Mech 1981, Keith 1983, Fuller 1989). On Isle Royale, about 20 - 25 resident wolves use the 544 km^2 island to hunt moose, yielding a density of 0.037 - 0.046 wolves/km^2 (Mech 1966, 1970; Pimlott 1975; Peterson 1977; Peterson and Page 1983). Pimlott (1975) believes this is about the highest sustainable density for wolves.

Nowak (1991) also reviewed wolf HR size and population densities, and arrived at similar generalities to the ones made here. From these compilations, I conservatively estimate that it takes at least 100 km^2 to support one wolf for energetic purposes, equivalent to a population density of 0.01 wolves/km^2. But it is not rare for populations to exist at densities as low as 0.002 wolves/km^2 or as high as 0.02 wolves/km^2.

I showed that Harestad and Bunnell's (1979) equation grossly overestimates HR in large carnivores, and that Damuth's equation has similar inadequacies estimating population densities. But using data from the previous discussion as a guide, I will make a rough estimate of exclusive HR size and population density for short-faced bears for use in subsequent discussions. A conservative (low) estimate will make the model more rigorous. Following that guideline, and pushing it further by assuming that *Arctodus* was foraging on a widely distributed food resource, a first estimate might be that each short-faced bear required 500 - 1000 km^2 of exclusive HR; probably closer to the latter. Since I am assuming that HRs are exclusive, this yields a population density of 0.001 - 0.002 bears/km^2. For purposes of this

model, I will use 0.001 bears/km^2 because it will err on the side of rarity.

As an additional consideration, Sandell (1989) observed three key patterns relating HR size to food distribution in solitary carnivores, which I will use to further narrow my estimates for *Arctodus*: 1) HR size, at least for females, seems to be determined by the abundance and distribution of food biomass during the most critical times of the year, such as during gestation and lactation. When food is abundant but not widespread during critical times, this leads to smaller HRs. 2) HRs will be exclusive when food resources are stable and evenly distributed; they overlap when there is much temporal variation in food supply, and 3) Exclusive HRs will be smaller than overlapping HRs. In discussions at the end of this paper, I will be showing why it is likely that short-faced bears had large HRs with a fair amount of overlap because carcasses would have been widely dispersed and seasonally scarce. Sandell also recognized two ways that solitary carnivores are spatially arranged which are relevant to this discussion: 1) because males are larger and require more energy, their HR is usually larger than females. 2) males will keep to territories when females are evenly distributed; when females roam, so do males. 3) male HRs do not overlap when females are evenly and densely distributed. 4) when males roam, their HRs are largest and overlap more during mating seasons, but their foraging HRs are smaller than their overall HR. I will be working under the assumption that female short-faced bears were highly vagile because of the random and widespread distribution of their food resource (carcasses), and thus so were males. Males would have had larger HRs because of their size, but HRs would have overlapped considerably. Territoriality in males would have been nearly non-existent because females and carcasses would have been randomly and distantly distributed; there would have been little reward for a male which guarded a territory, since there would have been little predictability in where carcasses (or females) would occur, and it would have been energetically inefficient to guard such a huge area. The only thing worth guarding was a carcass, and, for the most part, they are small, ephemeral, and their location is not permanent. All of these factors lead me to predict that the short-faced bear had a very large HR somewhere on the order of 1000 km^2.

Earlier, I estimated that the average short-faced bear (700 kg) needed to consume 5853 kg of flesh per year. If its HR was 1000 km^2, this necessitates that its habitat had to produce 5.85 kg flesh/km^2/year. These numbers mean that, on average, a short-faced bear had to encounter 100 kg of edible carrion every 6.25 days (consuming 16 kg per day).

Minimum Viable Population

Even if it can be shown that the Beringian system was able to produce 5.85 kg flesh/km^2/year, the question that arises is whether a population density of 0.001 short-faced bears/km^2 represents a minimum viable population— that is, one that is able to resist chance extinction. Goodman (1987), in fact, has developed a method for predicting the probability of chance extinction in a species over time based on its

body size and variability in its growth rate (r). Goodman's method actually estimates the minimum breeding population size (N_m) required for a species to have a 95 % chance of surviving chance extinction every 1000 years. Belovsky (1987) expanded the method by taking into account the influence of environmental variability on a species' r. In this modified model, Belovsky derived two allometric equations relating body mass to N_m, one for species with high variance in r and one for species with more constant r:

$$N_m = 409.540\ M^{-0.36} \quad \text{(species with high variance in } r\text{)} \qquad (27)$$

$$N_m = 19.018\ M^{-0.40} \quad \text{(species with low variance in } r\text{)} \qquad (28)$$

The two equations yield vastly different results, so it is important to have information about r. For instance, with an average mass of 700 kg, these two equations predict *Arctodus* would have required a minimum breeding population size of either 38,731 (Equation 27) or 1384 (Equation 28). When addressing variation in r, Belovsky was mainly concerned with how much r is influenced by variation in environmental and climatic factors. Within a given bear species, reproductive output varies and variation is correlated to environmental factors (Bunnell and Tait 1981), but in general bears are conservative breeders and their population growth rates do not seem tightly linked to levels of climatic variation. Therefore, I would expect a value for N_m in *Arctodus* to be closer to the lower value.

For the sake of these calculations, I will consider all the short-faced bears in eastern Beringia to constitute a single population (In comparison, Farlow (1993) made similar calculations for carnivorous dinosaurs and considered all individuals inhabiting the entire continental United States to be one population). Using maps in Hopkins *et al.* (1982) I estimate that unglaciated eastern Beringia was about 2,000,000 km^2. A minimum breeding population of 1384 bears would yield a density of one bear per 0.0007 km^2. My density estimate of 1 bear per 1000 km^2 (0.001 bears/km^2) requires a population of 2000 bears in eastern Beringia— a number not far from 1384. In comparison, a population of 38,000 bears yields a density of 1 bear per 53 km^2 (0.02 bears/km^2) — an unrealistically high density for such a large carnivore.

It is important to place some perspective on the numbers just calculated. First, 2000 individuals in all of eastern Beringia is a very small number. For comparison, the population of brown bears in Alaska today is estimated to be around 29,000 - 40,300, not including Kodiak Island; another 6000 - 7000 bears inhabit the Yukon Territory (Brown 1993). This is just about equal to the average value predicted by Belovsky's two equations (assuming 200 kg mass). Therefore, because brown bear populations in these areas are well above minimum breeding numbers, this is a good reason to suspect that the second equation (low variation in r) is the better predictor of minimum viable population size in bears. Still, 2000

TABLE 14. Carcass requirements of an average short-faced bear (700 kg) in eastern Beringia (an area of 2,000,000 km^2) and necessary carcass densities as a factor of population size

	population size (bears/km^2)		
energetic parameter, per individual bear	**2000 (0.001)[1]**	**4000 (0.002)**	**20,000 (0.010)**
size of mutually exclusive home range (km^2)	1000	500	100
required annual carcass production (kg/km^2/year) [2]	5.85	11.70	58.53
equivalent in carcass *numbers / densities* [3, 4]			
(average distance between carcasses)[5]			
small caballine horse (175 kg x 75 %)	45 / 0.045 (22.2)	45 / 0.090 (11.1)	45 / 0.450 (2.2)
bison (650 kg x 75 %)	12 / 0.012 (83.3)	12 / 0.024 (41.7)	12 / 0.120 (8.3)
mammoth (3800 kg x 75 %)	2 / 0.002 (500)	2 / 0.004 (250)	2 / 0.020 (50)

[1] minimum viable breeding population, estimated in text

[2] assumes an average bear weighs 700 kg, and requires 5853 kg of carcass flesh per year (= 16 kg per day) according to equation in text

[3] number of carcasses required by a single bear per year; density of carcasses expressed as number of animals per km^2

[4] carcass masses are reduced by 25 % to reflect non-caloric body parts — see text

[5] calculated as the inverse of carcass density

short-faced bears seems like a very small number.

Table 14 shows the density of carrion, and its equivalent in large mammal carcasses, required to support a population of 2000, 4000, and 20,000 short-faced bears in eastern Beringia (densities of 0.001, 0.002, and 0.010 bears/km^2 respectively).

3. Modeling Carcass Abundance

Next, I address the rate at which carcasses were produced on the Beringian landscape, in order to see if any of the population densities depicted in Table 14 can be supported. Keep in mind that I am testing the hypothesis that *Arctodus* made a living just by foraging on available carcasses, without killing any prey itself. Carcasses therefore should be available from two sources: predation by other carnivores and natural mortality among large herbivores.

Carcass Production from Predation

A good modern analog for mammalian communities or predator-prey relationships of Pleistocene east Beringia does not exist. In addition to short-faced bears, fossils of large carnivores from the region include wolf (*Canis lupus*), lion (*Panthera leo atrox*), brown bear (*Ursus arctos*), wolverine (*Gulo gulo*), scimitar (sabertoothed) cat (*Homotherium serum*), and dhole (*Cuon alpinus*) (listed in order of descending abundance). Cheetah fossils (*Miracinonyx trumani*) are not known from the region, but this predator must have occupied Alaska and Yukon for some period of the Pleistocene, since its fossil relatives are known from both sides of the Bering Strait, and the origin of the cheetah clade probably lies in North America (Adams 1979; Kurtén and Anderson 1980; Harington 1977, 1978; Van Valkenburgh *et al.* 1990).

Recently, (Matheus 1998, next chapter) I examined the carnivore guild of eastern Beringia and compared it to other guilds in the Pleistocene Holarctic. There, I made the assertion that it is unlikely that more than three or four of these large carnivores inhabited the region at any given time during the mid to late Pleistocene (also see Harrington 1977, 1978; Guthrie 1990a). Fossil abundances also lead me to conclude that wolves and lions were the only significant, long-term, predators that occupied eastern Beringia during the late Pleistocene (see next chapter). The other carnivores listed above either are not significant predators (brown bear, wolverine), or appear to have a limited (or at least unknown) chronological range in Beringia (scimitar cat, dhole, cheetah). I discuss predation in lions and wolves in detail below, but first I will make brief comments on the other species.

Brown Bear: Brown bears migrated to eastern Beringia from Asia probably in the early Wisconsinan (Kurtén 1960, 1963, 1966a, 1968, 1973, 1976a; Kurtén and Anderson 1974, 1980; Guilday 1968; Harris 1985; Matheus 1995, 1998) but they should not be considered significant predators in the

system (Matheus 1995). Stable isotope analyses of fossil brown bears from eastern Beringia indicate that they ate mostly vegetation, but also varying amounts of terrestrial meat and even salmon (Matheus 1994, 1995). Today, no population of brown bears relies primarily on carnivory, even though predation and scavenging can be locally or seasonally important. Predation by brown bears on ungulates in Alaska, for instance, occurs mostly during the brief period of calving seasons when caribou, moose, and occasionally sheep are taken. At these times, brown bear predation can be intense, but brief, and the biomass harvested is relatively small (Magoun 1976, Murie 1981, Ballard 1982, Boertje *et al.* 1988, Gasaway *et al.* 1992). But being adept scavengers, brown bears will compete with other carnivores for existing carcasses throughout the year, and brown bears will cache and defend carcasses (Mysterud 1973, Magoun 1976, Ballard 1982, Magoun and Valkenburg 1996). Low population densities and their limited predation probably minimize the effect of brown bears on carcass economy on an ecosystem-wide scale.

Wolverine: Wolverines were minor members of the Pleistocene large carnivore guild. They are highly carnivorous and are adept at processing large mammal carcasses. They mainly operate as scavengers and exist in low population densities. While wolverines are somewhat predatory, and even can kill caribou, they are not significant predators of large herbivores. However, because of their abilities to find carrion and defend it voraciously, they would have been a competitor to any scavenger on the landscape (Rausch and Pearson 1972; Magoun 1985; Hornocker and Hash 1981).

Homotherium: *Homotherium*'s importance to the carcass economy of eastern Beringia is unclear, as their temporal and geographic range in the region is sketchy. *Homotherium* fossils are rare, however, and it is possible that these scimitar cats were extinct in Beringia before the Wisconsinan period (Harington 1977, Guthrie personal communication, Matheus 1998). However, in terms of sabertooths, both *Homotherium* and *Smilodon* would have coexisted with *Arctodus* in other areas of North America south of Beringia.

Dhole and cheetah: The abundance and temporal range of dholes and cheetahs in eastern Beringia is even more uncertain. At the moment there is no good evidence to suggest that they even coexisted in a guild with all or any of the previously mentioned species. Dholes are advanced cursorial social predators and adept processors of carcasses, but cheetahs are not. Substantial edible carcass biomass would have remained after a cheetah kill, and solitary cheetahs would have been easy to chase off of a carcass. Packs of dholes would have been more resistant.

Next I want to examine typical predation rates for eastern Beringia's two main predators, wolves and lions. I will examine not only normal rates of carcass production by these predators, but also rates of surplus killing in order to assess their potential to kill additional prey when other predators confiscate carcasses. But first, it is worth considering an example of extreme carcass production— that of spotted hyenas in Africa's Ngorongoro Crater, a system where predator and prey densities are high and where

predators take a very large percentage of the prey population each year (Kruuk 1972, Schaller 1972, Hilborn and Sinclair 1979).

Spotted Hyena: Kruuk (1972) calculated that 430 spotted hyenas in the 250 km^2 Ngorongoro ecosystem each consumed 2 kg of prey per day, including adults and calves of wildebeest, gazelle, zebra, and miscellaneous species for a total of 313,787 kg annually. (Kruuk made his calculation by totaling average weights for carcasses on which hyenas were observed feeding and dividing this by the number of resident hyenas; total animals consumed = 2331, average weight = 135 kg.) This equates to 9.3 carcasses of 135 kg each, or 1255 kg/km^2/year. But only about 62 % of this biomass was confirmed as being killed directly by hyenas; a good deal of the remainder probably was scavenged. Hyenas scavenge far less in the Ngorongoro Crater, however, than they do in the Serengeti. Assuming hyenas kill 70 % of their food, direct carcass production by hyena predation becomes 879 kg/km^2/year, which means that 376 kg/km^2/year still is being "produced" by other means (other predators and natural mortality) in this system.

Kruuk also notes that during certain seasons hyenas will kill a large surplus, and that hyenas in general are not limited by their ability to kill prey, but rather on seasonal prey abundance. In fact, in the Serengeti each hyena "consumed" 3 kg of prey per day (as opposed to 2 kg in Ngorongoro)[2] according to Kruuk (consumed is in quotes because Kruuk derived this value by dividing prey biomass by the number of hyenas— not all of this biomass is necessarily consumed). During wildebeest calving season, Kruuk recorded a daily carcass production of 5.4 kg/hyena in the Serengeti— more than double their daily needs.

The theoretical pilfering of 5.8 kg/km^2/year (the minimum requirement to support short-faced bears) of the hyena's prey in the Ngorongoro would represent only 0.7 % of the edible carcass mass produced directly by hyena predation. However, the density of prey and predators in the Ngorongoro, and tropical savannahs/grasslands in general, is exceptionally high (Petrusewicz 1967, Kruuk 1972, Schaller 1972, Sinclair and Norton-Griffiths 1979). Furthermore, there are other carnivores competing with hyenas for their carcasses. But these predators also add more carcasses to the system. More will be said on hyena losses in the following discussion on lions.

Lion: Guthrie (1990a) states that lions probably were Beringia's most prevalent carnivore, but based on the number of fossils in the Alaska collection of the American Museum of Natural History I would argue that wolves may have been just as common, or more so. Lions are highly predatory but they turn heavily to scavenging when it is profitable (Kruuk 1972, Schaller 1972). They also are good processors of carcasses, but not on par with hyenas (Kruuk 1972; Ewer 1973; Van Valkenburgh 1989,

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[2] It is unclear how much of this discrepancy is due to methodological errors or the likelihood that hyenas in the Serengeti have higher energetic costs because they commute long distances to hunt on migratory prey, whereas hyenas in the Ngorongoro Crater do not (Kruuk 1972, Hofer and East 1993a).

1996).

Schaller (1972) found that lions in the Seronera area of the Serengeti consume approximately 2500 kg of prey per lion annually, yielding a daily individual consumption rate of 6.8 kg. The mean body mass of five female and 14 male lions weighed by Schaller was 166 kg. For this weight, the expected daily food consumption predicted by Harestad and Bunnell's equation (Equation 22) is 6.0 kg per day. Schaller was able to confirm that 75 % of this 2500 kg was killed directly by lions, while 16 % definitely was scavenged and 9 % was of uncertain origin. At 75%, it is reasonable to assume that each lion kills 5.1 kg of its own food per day, or 1875 kg annually (variations in edibility rates do not need to be accounted for because Schaller reports actual consumption).

Schaller estimates that about 2,000 - 2400 lions (including nomads) live within the 25,500 km^2 Serengeti ecological unit, for a density of one lion every 10.6 - 12.75 km^2, or 0.078 to 0.094 lions/km^2. That means lions in this system are producing up to 176 kg/km^2/year (1875 kg/lion/year x 0.094 lions/km^2), which can be considered an extreme rate because of the high density of lions. Kruuk (1972) reports densities for lions in Ngorongoro in the range of 0.12 - 0.23 lions/km^2, the highest anywhere, but Nowak (1991) compiled data from numerous more recent studies in the Serengeti and estimates an average density of 1 lion every 10.0 - 12.7 km^2, or 0.01 - 0.08 lions/km^2, including nomadic individuals. Using Nowak's average value, annual carcass production from lion predation would be roughly 166 kg/km^2/year. Removing 5.8 kg/km^2/year from this theoretical average system by scavenging would represent only 3.5 % of the lions' kill.

Schaller provides little data on the biomass of surplus killing by lions, but states that 1.4 - 4 % of wildebeest and zebra killed by lions (by far the two most common prey species for lion) were left uneaten or mostly whole (for unknown reasons). Extrapolating from his data on total prey killed (and subtracting 25 % for inedible material), this represents nearly 20 - 56 kg/lion/year, or 3.2 - 11.2 kg/km^2/year of surplus uneaten prey (20 kg/lion/year x 0.16 lions/km = 3.2; 56 kg/lion x 0.20 lions/km^2 = 11.2). These "scraps" represent only 0.9 - 3.0 % of the lion's normal kill rate, but represent practically the entire annual requirement of a population of short-faced bears (assuming each bear has an exclusive HR of 1000 km^2). Schaller also states that whole, untouched carcasses can be found on the Serengeti landscape (mostly in wooded areas) but he gives no estimate of their biomass or density. (Blumenschine (1987) studied carcass availability in Serengeti, but he also did not record data on biomass. His study examined carcass longevity.)

Some additional surplus killing from lions could be expected because of losses to other large carnivores, especially spotted hyenas. In general, however, lions tend to be dominant over other carnivores. The fact that hyenas engage in substantial surplus killing also suggests that predators in general are capable of killing at higher rates when forced to do so by competition. Consider further that

hyenas in Ngorongoro nearly double their predation rate during wildebeest calving season when prey are easy to come by (Kruuk 1972). Hyenas normally lose 21 % of their kills to lions in Ngorongoro, according to Kruuk, and in 63 % of these cases lions make off with a substantial part of the carcass. This means hyenas in Ngorongoro need to kill about an additional 15 % because of losses to lions. Recall that the normal predation rate in these hyenas is about 879 kg/km^2/year. Therefore, hyena losses to lions in the Ngorongoro Crater are about 132 kg/km^2/year. This is about one third of the lions' diet, which is right in line with Kruuk's estimates for scavenging rates by lions in Ngorongoro. In the Serengeti, lions kill a much larger proportion of their own food, and hyenas lose fewer kills to lions. I will show below that a roughly analogous competitive relationship exists between brown bears and wolves in Alaska.

Now I want to cautiously extrapolate some of this information about modern lions to Pleistocene lions in Beringia. Guthrie (1990a) provides compelling evidence that Beringian lions formed small prides or even hunted alone or in pairs as do some modern nomadic lions. He cites data in Van Orsdal *et al.* (1985) which shows that pride size correlates positively with prey density and territory size correlates negatively with prey density. Since Guthrie (1990a) argues that herbivore population densities would have been low in Beringia, it follows that lions would have formed small social groups that occupied large territories. Guthrie also uses paleolithic paintings in Europe as an indication that lions formed small groups. He shows that where lions live in high densities today, males have elaborately developed social organs because competition to control prides is intense (social display organs advertise condition and status). But paleolithic paintings depict males with small manes, and they frequently show scenes of males and females hunting together. Today males primarily hunt cooperatively with females only when pride associations are loose and when individuals are somewhat nomadic (Bertram 1975). The notion that Pleistocene lions hunted in pairs or alone also is supported by observations of fossil frequencies at Rancho La Brea. There, equal numbers of male and female lions representing all age classes are found (Jefferson 1992). If these lions had formed prides, one would not expect such a good cross-section of the population, but rather some sort of biased sampling— perhaps more young dispersing males or old infirm males looking for an easy meal, since both are excluded from access to female-killed carcasses in modern populations that form prides.

According to data summarized in Nowak (1991), modern nomadic lions typically form groups of 2 to 4 individuals, and such a pride may occupy an area as large as 4000 km^2 (at the extreme). For the sake of calculations, I will work off of Guthrie's arguments and make the conservative assumption that lions in Beringia were nomadic and that 2 lions hunted together over an exclusive territory of 500 km^2, for a density of 0.004 lions/km^2. For perspective, this equates to only 8000 lions in all of eastern Beringia and is 1/100 the density of Serengeti lions; Equation 28 predicts a minimum viable population size of 2438 lions in Beringia, assuming an average mass of 170 kg. From the previous calculations, each lion is

predicted to consume 2500 kg of prey each year. Assuming that scavenging opportunities for lions were limited (because of *Arctodus*), nearly all of this 2500 kg would have had to come from predation, yielding a carcass production rate of 10 kg/km^2/year. It was shown that hyenas can double their kill rate during calving seasons, and can be induced to kill at least an extra 15 % when they loose carcasses to a dominant carnivore. Below, it will be shown that wolves can be forced to increase predation by nearly 50 % in areas where brown bears steal carcasses. Therefore, under the assumption that Beringian lions could be forced to increase predation rates by a minimum of 20 %, we might expect them to minimally provide an additional 2.0 kg/km^2/year under pressure from a dominant carnivore such as *Arctodus*.

Wolf: In northern North America today, wolves are the most significant predators of large herbivores. (Puma rely heavily on deer and elk in western North America, but this predator typically does not exist in high densities.) In the arctic and subarctic of North America, wolves typically exist in low densities compared to wolves farther south (see earlier discussion). In these northern regions caribou are the wolf's main prey in tundra habitat, whereas moose are the its primary prey in the taiga. In the southern part of their range, wolves mainly hunt white-tailed deer but also moose in some areas. In terms of understanding secondary productivity in Pleistocene Beringia, data from these systems will be highly instructive, and comparable in some ways with a few qualifications.

I discussed earlier how pack sizes in arctic wolves preying on caribou are highly variable, and population densities are low— as low as 0.002 wolves/km^2 on the arctic coastal plain. Area-wide densities seem to be on the order of 0.003 wolves/km^2 (around 1 wolf per 300 - 400 km^2), but areas that provide better wolf habitat in the arctic support densities near 0.01 wolves/km^2. As a generality, arctic wolves kill a caribou about once every 4 days, and a moose every 7 days if moose are available. Wolf densities for the arctic coastal plain and northern foothills of the Brook Range are around 1 wolf per 350 - 450 km^2 (Stephenson and James 1982, ADFG Wolf Report 1994, Stephenson 1978, Ballard *et al.* 1990, Haber 1977, Murie 1944, Peterson 1977, Dale 1993).

In a study of two wolf packs in northwest Alaska, Stephenson and James (1982) found that caribou constituted 96 - 97 % of their prey biomass. Collectively, these packs hunted over an area of 2600 km^2, and killed a caribou every 3 - 4 days on average (mostly adults; $\bar{x}$ mass = 104 kg), for a total of about 10,846 kg/year, or 4.2 kg/km^2/year. Figuring in a 75 % edibility factor, the realized values are 8135 kg/year and 3.1 kg/km^2/year. This is a fairly typical kill rate for wolves feeding on large cervids (Mech 1966, 1970; Peterson 1977; Peterson *et al.* 1984; Fritts and Mech 1981; Ballard 1982; Ballard *et al.* 1987). Wolf densities in the region were 1 wolf per 390 km^2, so this amount of predation represents the activities of about 6 wolves, for a realized average of 1356 kg/wolf/year, or 3.7 kg/wolf/day.

In the same study, Stephenson and James measured actual consumption rates (as opposed to kill rates) for a 4 month period, during which the wolves were observed eating 1861 kg of adult caribou

Extrapolating this value for the remainder of the year (1861 kg x 3), the consumption rate becomes 2.5 kg per wolf per day, or 2.1 kg/km^2/year. This seems like a very accurate estimate of daily meat consumption since it agrees with results from other studies (Pimlott *et al.* 1969; Mech 1970, 1977; Kolenosky 1972; Peterson 1977; Peterson *et al.* 1984; Fritts and Mech 1981; Ballard 1982; Ballard *et al.* 1987) and it is 91 % of the value predicted by Equation 22 (2.3 kg/day for a 40 kg carnivore). This is very close to the actual percentage of caribou in the diet of these wolves noted above (96 - 97 %).

If annual predation is 3.2 kg/km^2/year and consumption is 2.1 kg/km^2/year, then approximately 1.1 kg/km^2/year of surplus carcass biomass is produced by these low density predators. This is a little less than the amount of surplus predation I predicted for a population of Beringian lions.

Today, grizzlies, wolverines, foxes, and ravens consume surplus carcass biomass in northern Alaska and Canada (Magoun 1976, Murie 1981, Carbyn *et al.* 1993), but competition generally is less intense compared to other carnivore systems I discussed, mainly because carnivore densities are low in northern North America. Ballard (Ballard 1982, Ballard *et al.* 1981) conducted a study on wolf-grizzly interaction and predation rates on moose in the Nelchina Basin of southcentral Alaska where competition for carcasses between these two carnivores can be intense. He noted two important patterns. First, areas with high moose densities had higher wolf densities but lower levels of wolf-grizzly competition for carcasses, compared to areas with low moose densities (grizzly density did not vary). Second, wolves increased their predation rates in areas where they lost carcasses to grizzlies.

Ballard (1982) reports that the carcass biomass produced by Nelchina wolves in all areas was around 4.6 kg/wolf/day, but in areas with competition, wolves had to produce 6.2 kg/wolf/day — an increase of nearly 50 %. These are numbers calculated by Ballard, and already reflect the 75 % edibility of carcasses. Two packs of wolves (7 and 8 individuals) foraged over a combined area of 1399 km^2 yielding an effective average density of 1 wolf for every 93 km^2; wolf density for the entire Nelchina basin below 1200 m is around 100 wolves/km^2. Using the later value and the two predatory rates above, annual carcass production would be at least 16.8 kg/km^2/year in low competition areas and 22.6 kg/km^2/year in high competition areas. This yields a surplus predation rate of 5.8 kg/km^2/year induced by the loss of carcasses to grizzlies. Even 16.8 kg/km^2/year in areas of low competition is equivalent to nearly 8 kg/km^2/year of surplus production, assuming that wolves require around 2.3 kg of meat per day. Therefore, carcass production, in general, is higher in the Nelchina Basin than in northwest Alaska because both predator and prey densities are greater in the Nelchina Basin (see arguments in Fuller 1989).

In areas of southern Canada and the northern contiguous U.S. states, wolves feed mainly on white-tailed deer, but also varying amounts of moose. In these areas, wolf packs average about 4 - 8 individuals and area-wide wolf densities are around 0.02 wolves/km^2, or 1 wolf per 50 km^2. Exclusive pack territories are approximately 200 km^2, or around 33 km^2 per wolf, and they kill a deer about once

every 3 -4 days ($\bar{x}$ mass = 50 kg) (Mech 1970, Pimlott 1969, Fritts and Mech 1981, Nelson and Mech 1981, Fuller 1989, Keith 1983). Studies in these southern areas of the wolf's range also confirm that an average wolf eats a little over 2 kg of meat per day.

It is informative to note that, in the southern part of their range, the sizes of wolf packs do not differ much among packs that hunt moose and packs that hunt white-tailed deer (Mech 1970). However, the population density of wolves that hunt moose (in the south) can be greater than those that hunt white-tailed deer. As an extreme example, wolf densities on Isle Royale average around 0.04 wolves per km^2, or 1 wolf per 25 km^2. Wolves in this system typically kill 13 - 19 % of the moose population per year and kill a moose every 3 days. This feeds 18 - 20 individuals (pack sizes are unusually high on Isle Royale), so assuming a modest average moose mass of 300 kg, wolves on Isle Royale produce at least 46.8 kg/km^2/year of carcass mass annually, equivalent to approximately 1.9 kg/km^2/year of carcass production from each wolf (Mech 1966, 1970; Jordan 1970; Peterson 1977). In the north (Alaska and northern Canada), wolves that feed on moose have densities 2 -3 times lower than wolves that feed on moose in the south. Moreover, northern wolves feeding on caribou have densities that are about 1/10 of those in the south (Mech 1970; Ballard 1982; Ballard *et al.* 1981, 1990; Stephenson and James 1982; Oosenbrug and Carbyn 1982; ADFG Wolf Report 1994).

Using these generalities, it is possible to infer certain aspects of wolf densities and predation on the mammoth steppe of Pleistocene east Beringia. With the presence of lions, it is quite possible that wolves were competitively excluded from utilizing some larger prey which they otherwise would have been able to hunt. This may explain why late Pleistocene wolves in Beringian were smaller than present (Matheus 1998, next chapter). If wolves were smaller-bodied and were hunting smaller prey, they probably existed in higher densities during the Pleistocene, but in order to remain conservative (i.e., emphasize minimum values) in my calculations, I will assume an approximate wolf density of 1 wolf per 300 km^2 in eastern Beringia (0.0033 wolves/km^2) — similar to area-wide densities in the modern arctic.

I showed that wolves require about 2.5 kg of meat per day (912.5 kg/year) but they kill about 3.0 - 3.5 kg of meat per day (1095 - 1277.5 kg/year) in areas with little or no competition, yielding a surplus of about 100 - 365 kg/wolf/year (11- 40 %). Assuming a modern density of 0.01 wolves/km^2, the typical northern wolf population today provides (in principle) approximately 1.0 - 3.7 kg/km^2/year to scavengers. In my theoretical, modest Beringian population with 0.0033 wolves/km^2, the normal surplus (i.e., without competition) is predicted to be 0.33 - 1.2 kg/km^2/year. But I also showed that in areas where competition is high and wolves lose carcasses to bears, they can be induced to produce an additional 5.8 kg/km^2/year (in an area with a density of 0.01 wolves/km^2). Extrapolated to a hypothetical population with 0.0033 wolves/km^2 this equates to an additional surplus of 1.9 kg/km^2/year, for a combined total surplus of 2.3 - 4.9 kg/km^2/year from wolves— 1.0 - 3.7 kg/km^2/year from normal surplus, plus 1.9 kg/km^2/year from

induced predation. These estimates are very conservative.

Earlier, I showed how Beringian lions might be expected to provide a surplus of at least 2.0 kg/km^2/year when pressured by competition from a dominant carnivore. According to these conservative estimates, *the two primary predators of the Mammoth Steppe could collectively produce at least 4.9 - 7.6 kg/km^2/year of edible carcass biomass* (reductions for inedible carcass mass were made in the initial calculations). This would have been just about the right amount of biomass to support a minimum viable population of short-faced bears.

Carcass Production from Natural Mortality

1. Modeling Herbivore Populations in Eastern Beringia

The preceding calculations show that the predatory actions of wolves and lions alone could arguably support the dietary needs of a minimum viable population of scavenging short-faced bears in Pleistocene east Beringia. I was conservative throughout these estimates, but they still cannot be considered to be very precise. Furthermore, reflecting on the densities of other large mammals today, it is not completely convincing that a density of 1 short-faced bear per 1000 km^2 constitutes a viable breeding population. Therefore, evidence of additional carcass production is necessary for the scavenging hypothesis to be accepted as wholly credible.

So far I have made no consideration of natural mortality in herbivore populations— a factor which certainly would have been adding carrion to the system. A thorough modeling of ungulate population dynamics is beyond the scope of this paper, and I think it is necessary only to estimate the general magnitude of carrion being produced by the system through natural mortality. Furthermore, whereas Pleistocene carnivore population dynamics have not been modeled, attempts have been made to qualitatively and quantitatively model Pleistocene herbivore populations and secondary productivity. I will discuss and modify two such models— Redmann (1982) and Bliss and Richards (1982). Both were designed to address the issue of secondary productivity in Beringia, but I believe there are shortcomings in each one: Redmann stopped short of making specific estimates for Beringia; his model was more a reflection of productivity in northern grasslands. Bliss and Richards were primarily interested in determining how many humans could be supported by the Beringian landscape, so they modeled harvestable levels of big game. While Bliss and Richard's model sounds very applicable to the issues in this paper, I think there are serious flaws with its assumptions about ecosystem structure and function on the Mammoth Steppe of eastern Beringia, as well as the data they use to establish input parameters.

Redmann's (1982) Model: Redmann's model estimates the biomass density of large herbivores in a northern grassland using the following conditions and assumptions: 1) primary productivity of edible above ground biomass is set at 150 kg/km^2/year; this is the amount of forage ("herbage" in Redmann)

available to herbivores and is a conservative approximation based on productivity rates measured in modern cold-temperate grasslands, 2) a positive linear relationship exists between the rate of forage production and herbivore biomass density, 3) annual consumption (C) by herbivores scales to body mass (M) in a manner consistent with metabolic scaling:

$$C = 32.85\ M^{0.75} \tag{29}$$

4) energy is the only dietary factor limiting secondary production; protein and other nutrients are not limiting, 5) energy (herbage) is available throughout the year. Redmann's model is a general predictor for north temperate grasslands, and some of its assumptions will have to be adjusted to fit Beringia.

The key element of this model is that it accounts for observations that herbivore biomass and diversity are strongly influenced by levels of species dominance in the community. When a large-bodied herbivore dominates, higher overall biomass is achieved, but most of it is allocated to the dominant species. The lowest biomass occurs in herbivore communities dominated by a small-bodied species.

Redmann uses his model to predict the biomass density for five theoretical northern grasslands, each with the same five herbivore species but at different levels of dominance (relative density): 1) strong dominance by a large species, 2) strong dominance by a small species, 3) weak dominance by a large species, 4) weak dominance by a small species, and 5) no dominance. When one large herbivore dominates the system, 150 kg/km^2/year of herbage production yields a standing herbivore biomass density of 13,500 kg/km^2, of which 84 % is in the form of the dominant species. The other four scenarios in Redmann's model yield 6720, 12,000, 8300, and 10,200 kg/km^2/year respectively.

The first estimate, based on a dominant large herbivore, yields an unrealistically high density for Beringia, since equivalent levels in modern ecosystems only can be found in tropical grasslands and savannahs and in one ecosystem in Alberta (see Table 15). The system modeled in this scenario might resemble the community dominated by bison on the far northern great plains of Canada 200 years ago. Past great bison herds of the plains have been estimated to have densities on the order of 10 - 14 bison/km^2 (Seton 1909, Roe 1970, McHugh 1972, Dary 1974), but Redmann's equation predicts approximately 25 bison/km^2, assuming that the average bison weighed 450 kg (modern weight) and that bison constituted 84 % of the system's biomass.

Redmann's scenario which assumes no dominance may be more appropriate than one which assumes the presence of one large dominant species because there were three co-dominant herbivores in Beringia — mammoth, bison, and horse. The "no dominance" scenario predicts a somewhat reduced herbivore biomass of 10,200 kg/km^2. One possible way to distribute this biomass would be among 1

TABLE 15. Large mammal standing biomass densities of modern ecosystems and the predicted density for late Pleistocene east Beringia

ecosystem (type of biomass reported)	large mammal biomass (kg/km^2)	source
entire Serengeti Plain (large herbivore prey)	annual x̄ = 4222 seasonal range = 998 - 7234	Schaller 1972
woodlands of western Serengeti (large herbivore prey)	3110	Bell 1967 (in Schaller 1972)
savannah of Kruger Park (large herbivore minus elephant)	7785	Schaller 1972
savannah of Kruger Park (large herbivore minus elephant)	9000	Watson and Turner 1965 in (Schaller 1972)
grassland/savannah of Ngorongoro Crater (large herbivore prey)	16,200	Kruuk 1972
Ruwenzori Park, Uganda plains-tropical forest ecotone (large herbivores— including many elephants/hippos)	20,000	Eltringham 1974 (in Redmann 1982)
boreal forest of Alberta (large herbivores)	5700	Telfer and Scotter 1975 (in Redmann 1982)
semidesert of southcentral Russia (saiga biomass in a protected park)	5200	Bannikov 1967 (in Redmann 1982)
grassland of South Dakota (large herbivores)	3640	Petrides 1956 (in Redmann 1982)
grasslands of Nebraska (large herbivores)	919	Petrides 1956 (in Redmann 1982)
parkland of Alberta (large herbivores)	2530	Flook 1970 (in Redmann 1982)
dry tundra of St. Elias - Kluane region, Yukon (large mammals)	89 (actual estimated) 175 (potential estimated)	Geist 1978 (in Redmann 1982)
tundra of Southampton Island, Northwest Territories (caribou)	36	Parker 1975 (in Redmann 1982)
alpine tundra of southern Norway (caribou)	233	Ostbye 1975 (in Redmann 1982)
southern boreal forest on Isle Royale (moose)	401	calculated from data in Mech 1970
northern boreal forest of interior Alaska and Yukon (moose)	9 - 289 (assumes x̄ moose = 200 kg)	calculated from data in Gasaway *et al.* 1992
tundra of Alaskan arctic slope (caribou- Western Arctic Herd)	91 (assumes x̄ caribou = 100 kg)	calculated from data in Ballard *et al.* 1990
tundra of southcentral Alaska (Nelchina Basin) (large mammal)	< 300	Guthrie 1968
Mammoth Steppe of Eastern Beringia (total large herbivore biomass)	1000	models revised in this study

mammoth (3800 kg), 4 bison (2600 kg), and 15 caballines (2650 kg), along with 1175 kg of other less common herbivores on each km^2 of Beringia. If only bison were present, their density would be nearly 16 bison/km^2 — as dense as the former herds on the great plains. These values still seem unreasonably high and exceed the biomass densities given by Redmann himself for many modern temperate grasslands.

Redmann sets annual herbage production at 135 kg/km^2/year in all scenarios of his model. However, it may be unrealistic, and unnecessary, to invoke such high rates to account for high levels of secondary productivity in Pleistocene Beringia, and even though Redmann's estimate is conservative for grasslands, it probably is too high for Beringia. Secondary productivity and herbivore diversity in Beringia are best explained by models relying on increased digestibility and extractable nutrition in Pleistocene vegetation (i.e., increased consumption efficiency and assimilation efficiency in herbivores), along with staggered spikes in the timing of green-up, a longer growing season, and increased habitat heterogeneity (Guthrie 1976, 1982, 1984a, 1984b, 1990a, 1990b). This assessment of Guthrie's casts doubt on two assumptions in Redmann's model: 1) that energy (herbage) is available all year, and 2) that energy, not protein, is the limiting factor determining biomass density. While the first assumption is necessary to keep the model manageable, and it is a standard assumption when comparing ecosystems, Guthrie's arguments show that the timing and duration of available high quality forage probably are the key factors regulating populations in Beringian mammals, past and present. High quality forage means high protein forage, and it is protein, not energy, that limits herbivore populations (Janis 1976, Hanley 1980, Robbins 1993).

Moreover, biomass density is not equivalent to population density (i.e., number of individual animals), and Guthrie's model mainly addresses patterns not of biomass quantity, but biomass distribution and its impact on mammalian body sizes. At an ecosystem level, however, a population composed of fewer, but larger, individuals is energetically "more efficient," and it would take less energy to maintain such a population. Therefore, a greater diversity of species can be maintained for a given amount of trophic energy if their average body size is larger and population numbers are fewer.

The above arguments suggest that it is best to use a cautious, conservative, estimate of secondary productivity in Beringia when calculating the carcass biomass produced by natural mortality. Since Redmann's estimates appear too high for Beringia, I will use half his value— 5100 kg/km^2/year— and examine the herbivore populations this could support. To do so, I need values for the division of biomass in the system. Guthrie (1968) estimated the relative biomass of Pleistocene large mammals from four sites in Interior Alaska based on their fossil abundance, and derived the following biomass percentages for the top three herbivores: 46 % Bison, 33 % mammoth, and 17 % horse (averaged over the four sites). I will modify Guthrie's numbers slightly to reflect subsequent finds from around Beringia which suggest a higher frequency of minor taxa; the values I will use for relative biomass are 40 % bison, 30 % mammoth, 18 % caballines, and 12 % other herbivores. Table 16 shows the resulting population densities calculated

for this theoretical system assuming a total standing large herbivore biomass of 5100 kg/km^2/year. Results show that this system would simultaneously support population densities of 0.402 mammoth/km^2, 3.138 bison/km^2, 5.246 caballines/km^2, and still leave another 612 kg/km^2 divided between other minor species (e.g., caribou, muskox, saiga, elk, camel, etc.). This latter amount would support 2.5 individuals/km^2 of a species weighing 250 kg, for instance. Before estimating carcass production from natural mortality in these populations, I will check their validity using Bliss and Richard's model.

Bliss and Richard's (1982) Model: Bliss and Richards constructed a model of finer detail specifically for Beringia. Their model essentially takes the view that the Mammoth Steppe was a tundra biome, but with a higher percentage of dry sedge-grass tundra compared to today's northern tundra. Under this view, the Mammoth Steppe supported a more diverse and productive large herbivore community than today's ecosystem because dry sedge-grass tundra is the most productive type of tundra habitat. As I mentioned, the goal of these authors was to determine how much meat such a system could provide for humans, and in turn, whether this was enough to sustain a viable human population— a question very similar to the one I am addressing.

These authors began their reconstruction by collecting data on primary and secondary productivity in a variety of modern habitats in the arctic and subarctic, including well-drained upland sedge fields, tussocky tundra, shrubby tundra, alpine tundra, and sedge-moss meadows. Then, using published data on Pleistocene vegetation patterns, they reconstructed the percentages of these habitat types in a hypothetical Beringian river valley spanning 1000 km^2. Next, they used consumption data in analogous modern mammals to estimate the forage requirements of the system's predominant herbivores, which they concluded were mammoth, horse, bison, muskox, caribou, and moose (a conclusion which is not very accurate). Finally, they used modern values of net primary production (NPP) and consumability for each habitat, and extrapolated them to the presumed distribution of each habitat on the mammoth steppe, in order to estimate how much herbivore biomass would be supported for each species in each habitat. I will briefly review the results of their simulation.

Bliss and Richard's hypothetical system contained 65 % upland sedge-grass tundra, 20 % upland cushion plants (alpine tundra), 10 % wet sedge tundra (tussocky tundra), and 5 % tall willow tundra (shrub tundra). They estimated the amount of forage each herbivore would extract from each habitat based on their presumed diet and the ability of each habitat to provide for it. For example, mammoth were presumed to get 40 % of their forage from tall willow habitat, 40 % from wet sedge, and 20 % from upland sedge-grass. The amount of standing herbivore biomass and the predicted population density for each species is presented in Table 17. Bliss and Richard's model predicts about 75 % less standing biomass than the modified Redmann model (Table 16). Population numbers are difficult to compare

TABLE 16. Estimated population densities and total numbers of dominant large herbivores in eastern Beringia according to a modified biomass estimate using Redmann's (1982) model. Total biomass predicted by the modified model is 5100 kg/km^2, which was divided amongst each species according to relative biomass estimates modified from Guthrie (1968)[1]. Values generated from this model are considered much too high, as discussed in text. Compare values to those in Table 17 (Bliss and Richard's 1982 model) and Table 18 (values derived from this study).

species (mass in kg)	% of biomass [1]	resultant biomass density (kg/km^2)	resultant population density (animals/km^2)	total population in eastern Beringia [2] 2,000,000 km^2
mammoth (3800)	30	1527	0.402	804,000
bison (650)	40	2040	3.138	6,276,000
horse (175)	18	918	5.246	10,491,429
others ($\bar{x}$ = 250)	12	612	2.448	4,896,000

[1] Biomass percentages modified from Guthrie's (1968) estimates, which were based on fossil abundances at four sites near Fairbanks, Alaska. Guthrie's values were modified by the present author based on subsequent discoveries and data from a larger region.

TABLE 17. Estimated biomass, population densities, and total numbers of dominant herbivores in Pleistocene East Beringia according to the model of Bliss and Richards (1982). Biomass estimates come directly from the model; densities and population numbers calculated first using body weights given by Bliss and Richards, then using weight estimates from this study. Compare values to those in Table 16 (Redmann's model) and Table 18 (values derived from this study).

species	standing biomass density from model (kg/km^2)	body weight used by Bliss and Richards (kg) [1]	adjusted body weight used in this study (kg) [1]	population density per Bliss and Richards ($animals/km^2$)	population density using adjusted body weights ($animals/km^2$)	total population in Eastern Beringia per Bliss and Richards (= 2,000,000 km^2)	total population in Eastern Beringia using adjusted body weights (= 2,000,000 km^2)
mammoth	96 - 136	2230	3800	.043 - .061	.025 - .036	86,000 - 122,000	50,000 - 72,000
horse	84 - 236	150	175	.560 - 1.573	.480 - 1.349	1,120,000 - 3,146,000	960,000 - 2,698,000
bison	127 - 305	450	650	.282 - .678	.195 - .469	564,000 - 1,356,000	390,000 - 938,000
caribou	132 - 270	100	200	1.320 - 2.700	.660 - 1.350	2,640,000 - 5,400,000	1,320,000 - 2,700,000
musk ox	151 - 289	180	400	.840 - 1.605	.320 - .578	1,680,000 - 3,210,000	640,000 - 1,156,000
moose	209	300	400	.697	.523	1,394,000	1,046,000
total	799 - 1445						

[1] Body weights used by Bliss and Richards are weights from modern species or estimated from modern relatives. Adjusted body weights are those proposed in this study. Adjusted body weights only change estimates of population size and density, not biomass density.

TABLE 18. Conservative estimates of herbivore populations and carcass densities in late Pleistocene east Beringia, based on an overall herbivore biomass density of 1000 kg/km^2.

species (kg)	biomass density [1] (kg/km^2)	population density (no./km^2)	total population in eastern Beringia (2,000,000 km^2)	annual adult mortality rate (%)	edible carcasses from natural mortality = *carcass production minus 50%* [2] kg/km^2/year	no./km^2/year	km^2/carcass	edible carcass biomass from surplus predation [3]	total carcass biomass from predation and natural mortality [3]
mammoth (3800)	300	0.079	158,000	3	4.50	.0012	833	—	—
bison (650)	400	0.615	1,230,000	5	10.00	.0154	65	—	—
horse (175)	180	1.029	2,058,000	7	6.30	.0360	28	—	—
other herbivores	120	— [4]	— [4]	— [4]	— [4]	— [4]	— [4]	—	—
TOTAL	1000	1.723 [5]	3,446,000 [5]	—	20.80 [5]	.0526 [5]	19 [5]	**6.3** kg/km^2/year	**27.10** kg/km^2/year

[1] based on the following biomass percentages: bison 40 %, mammoth 30 %, horse 18 %, others 12 %
[2] 25 % loss assumed for inedible portions of carcass, 25 % loss due to losses to other carnivores and undiscovered carcasses
[3] calculating predation levels for individual species requires too many assumptions and is beyond the resolution of this model
[4] not an appropriate calculation unless species and weight are specified
[5] only includes mammoth, bison, and horse

between the two models because they were formulated in different ways, but these values and the total biomass value seem more realistic than the Bliss and Richard's model, and are close to my estimates using the modified Redmann model.

Bliss and Richards are highly regarded experts on the subject of productivity in modern tundra ecosystems, and while the numbers generated by their model may be agreeable, I have strong reservations about their assumptions regarding ecosystem structure and function on the Mammoth Steppe. Because a thorough critique of their model is beyond the scope of this exercise, I will only briefly outline my contentions here. First, while some authors, relying mainly on floral evidence, subscribe to the idea that the mammoth steppe was a modified tundra ecosystem (e.g., Schweger and Hapgood 1976; Cwynar and Ritchie 1980; Ritchie and Cwynar 1982; Colinvaux 1980, 1986; Colinvaux and West 1984; Ager 1982; Giterman *et al.* 1982; Schweger 1982), the idea has been strongly refuted by others (Guthrie 1968, 1982, 1984a, 1984b, 1990a, 1990b; Sher 1974, 1986; Matthews 1982; Yurtsev 1982). This latter group argues that the full glacial fauna of Beringia was dominated by herbivores which had evolved as grazing specialists, indicating the indisputable presence of a cold grassland (steppe) biome. Even though grassy elements grow in tundra environments, true grasslands are distinct from tundra and each is maintained by vastly different processes (Walter 1973, Tieszen and Detling 1983).

Therefore, Bliss and Richard's decision to use tundra analogs, especially to model energy flow, seems a poor choice. For instance, they use data on secondary productivity, consumption rates, and population turnover rates from modern tundra systems across arctic Alaska, Canada, and Russia, and they often rely on microtines as mammalian models for the conversion of primary productivity into herbivore biomass. Furthermore, as I emphasized earlier, the key to higher levels of secondary productivity in Pleistocene Beringia was not higher NPP; instead, more of the primary production was available to consumers— a trait of grasslands, not tundra. In these regards, Redmann's model is somewhat superior because it is based on grassland systems.

Combined Model: Despite their shortcomings, I will use the results of these two models to conservatively estimate that large-herbivore biomass (standing crop) in late-Pleistocene Beringia was in the range 1000 kg/km^2. Considering the level of production achieved in northern grasslands today, 1000 kg/km^2 is not unreasonable (Table 15). However, it is 3 to 10 times higher than what one finds in modern taiga and tundra systems (Table 15). Therefore, I will propose the following conservative, round-number estimates of herbivore standing biomass in late Pleistocene (full glacial) eastern Beringia using Guthrie's (1968) modified estimates of relative biomass (values also presented in Table 18):

mammoth **(3800 kg)**	**30 % of biomass = 300 kg/km² = .079 mammoths/km² = 158,000 total in eastern Beringia**
bison **(650 kg)**	**40 % of biomass = 400 kg/km² = .615 bison/km² = 1,230,000 total in eastern Beringia**
horse **(175 kg)**	**18 % of biomass = 180 kg/km² = 1.029 horse/km² = 2,058,000 in eastern Beringia**
others	**12 % of biomass**

2. Natural Mortality in Eastern Beringia

Natural mortality rates (used here to mean non-predatory mortality) are known for enough modern large mammals that it should be possible to estimate natural mortality for Beringian herbivores using the preceding population estimates.

Hilborn and Sinclair (1979) calculate that non-predatory mortality for adult wildebeest in Serengeti is 5 % annually in years without catastrophic die-offs, although Talbot and Talbot (1963) and Houston (1979) suggest it may be nearer 8 % and 12 %, respectively. Kruuk (1972) states that natural mortality for wildebeest living in Ngorongoro is somewhat higher than in the Serengeti, as is the population turnover rate as a whole. Zebra loose 3 % of the adult population annually to natural mortality, according to references cited in Kruuk (1972), and 16.5 % of the adult hyenas in his study died each year. Sinclair (1977) reports that adult African buffalo experience 4 - 12 % non-predatory mortality annually, and average around 8 %. In Manyara, Tanzania, a system where half the deaths are from hunting by humans, adult elephants suffer 3 - 4 % annual losses (Owen-Smith 1988). Owen-Smith presented similar mortality rates for other populations of elephants, and he suggested that they are somewhat higher than natural rates because of hunting. Over-all, Owen-Smith indicates that adult natural mortality in megaherbivores is around 2 - 5 % per year.

In the boreal forest of interior Alaska and the Yukon Territory, moose mortality varies depending on the populations' stability. Annual adult mortality is 6 - 6.8 % in steady or increasing moose populations, but as high as 19 % when populations are declining (Gasaway *et al.* 1983, 1992). In a five-year study on bison in the badlands of South Dakota, Berger and Cunningham (1994) found that adult bison experienced a maximum of only 3.2 % annual mortality. However, this is a protected system without significant predation, and bison numbers are increasing and well below carrying capacity. Bison mortality in natural systems must therefore be higher.

Earlier, I discussed ecological arguments which predict that Beringia's Pleistocene herbivores most likely existed in small populations of larger bodied individuals (following Guthrie 1984a). Species such as this, where more biomass is housed in fewer, but larger, individuals, tend to have relatively lower population turnover rates— that is, longer lifespans and lower mortality rates (Eisenberg 1981,

Hennemann 1983, Calder 1984, Owen-Smith 1988). Large-bodies species like mammoth and bison would have had even longer lifespans and even lower mortality rates. A general allometric model scaling mortality rates to body size does not exist, but many other life history parameters scale in accordance with metabolic scaling— that is, $\propto M^{0.75}$. This is believed to be the reason why longevity, for instance, scales reciprocally $\propto M^{0.25}$ (Calder 1984), and why the rate of population increase scales $\propto M^{-0.26}$ (Hennemann 1983). Calder also reviews data showing that age-specific death rate increases proportional to $M^{-0.25\ -\ -0.30}$. Since mortality is inversely proportional to longevity and should scale similar to the rate of population increase, it seems reasonable to generally assume that mortality scales nearly $\propto M^{-0.25}$.

Using this logic and the data listed above for mortality in modern mammals, I will calculate a rough approximation for annual adult mortality in mammoth, bison, and horse. Starting with a conservative assumed adult mortality rate of 5 % for the 800 kg steppe bison, and applying a -0.25 scaling constant (scaled to body mass), the rates in horse (175 kg) and mammoth (3800 kg) are predicted to be 7.2 % and 3.3 % respectively. But considering that both equids and proboscidian have conservative life history strategies relative to bison, it seems best to lower these latter two estimates somewhat. I will use values of 6 % for caballines and 3 % for mammoth.

Overlaying these mortality rates onto my population model, it is possible to estimate the rate of carcass production from natural mortality in each species. The results using conservative population estimates are shown in Table 18. Assuming a standing live biomass of 1000 kg/km^2, arrived at in the earlier discussion, the total carcass biomass resulting from natural mortality in all major large herbivores is estimated to be around 41.38 kg/km^2/year. As before, 25 % of this must be subtracted for the non-caloric portion of a carcass. It also seems prudent to subtract 25 % to account for carcasses that are partially consumed by other predators and carcasses which go undiscovered, leaving a total of 20.80 kg/km^2/year.

Adding my earlier estimates on surplus predation (average of 6.3 kg/km^2/year), *total carcass production on the Pleistocene landscape is predicted to be roughly 27.10 kg km^2 year. That is over four times the amount needed to maintain a minimum viable population of short-faced bears, thereby supporting the hypothesis that Beringian ecosystems could have sustained a 700 kg carnivore that obtained all of its meat through scavenging.* Terrestrial ecosystems of Pleistocene Beringia were far more productive than today, but they probably were less productive than most other ice-free regions of North America (Guthrie 1968, 1982, 1984a, 1984b, 1990; Hopkins *et al.* 1982). Therefore, from this "worst case scenario," it is plausible to argue that *Arctodus* could have functioned as scavenger across its entire range in North America.

3. Corollaries to the Model

Short-Faced Bear Population Levels: Throughout this modeling exercise, I started with a minimal viable population of scavenging short-faced bears and looked for ways that Beringia's Pleistocene ecosystem could support it energetically. Now that these conditions seem to be met, I will turn the issue around and ponder the maximum number of short-faced bears the ecosystem could support. If the annual requirements of a 700 kg short-faced bear was 5853 kg of carrion, then 27.10 kg/km^2/year of carrion should support an *Arctodus* density of ≈ 0.005 bears/km^2, equivalent to one short-faced bear every 200 km^2 or 10,000 bears in all of eastern Beringia. Considering *Arctodus*' size, these estimates are very much in line with densities of other large carnivores I discussed, and it supports my earlier prediction that *Arctodus* may have had an exclusive home range as small as 500 km^2. Relying on conventional wisdom, 10,000 bears in a 2,000,000 km^2 area seems like a much more reasonable population than 2,000— yet it still is not a lot, and I will be arguing later that a primary reason for *Arctodus*' demise may have been the inherent untenability of a carnivorous niche for such a large mammal due to the fact that it would be difficult for to maintain a minimal viable population density that still allowed each individual to extract enough energy from the ecosystem.

Predator-Prey Ratios: The model's estimates of secondary productivity also can be turned around and used to predict predator densities in Pleistocene Beringia. This also will provide a secondary test of my model, since one can ask whether the predicted densities seem realistic. Trophic principles dictate that carnivore numbers obviously will be far less than herbivore numbers (Slobodkin 1961; Clutton-Brock and Harvey 1978, 1983; Gittleman and Harvey 1982). Conventional wisdom is that ecological efficiencies in secondary consumers will be around 10 % (Slobodkin 1968, Pimm 1982), but Turner (1970) showed that they really are much lower— generally < 2 % in endotherms, with maximum values reaching about 3 %. Since the system in question is one of endotherm consuming endotherm, predator-prey biomass ratios should then be around 1:100. Ratios from actual vertebrate predators in terrestrial ecosystems often are lower than this (discussed below), but many certainly no longer represent natural systems. Because there is no regular, predictive pattern of predator size to prey size in nature, the numbers ratio of predator:prey (as opposed to biomass ratio) will have to be examined from empirical evidence.

Data in the Alaskan wolf studies cited earlier suggest a general wolf:prey numbers ratio of a little over 1:100 and a general biomass ratio of around 1:250, in areas where wolves experience some population control by hunting or management. Both ratios are higher (relatively more wolves) in areas without significant human control (data also reviewed in Keith 1983). On Isle Royale, the biomass ratio is very similar, although the number ratio is higher (≈ 1:30) because large-bodied moose constitute the vast majority of prey (on Isle Royale, wolves and moose are not hunted or controlled). In southern boreal

forests of Ontario and Minnesota, where deer are the main prey, predator prey ratios are about 1:100 - 1:150, but biomass ratios still are around 1:200.

Puma, North America's only other significant predator of large mammals, have extremely low numbers compared to their prey (Hornocker 1970). Numbers ratios are as low as 1:600, but approach 1:200 in more pristine areas (Nowak 1991). Respective biomass ratios are around 1:524 and 1:46 (puma frequently kill prey larger than themselves, leading to a higher biomass than numbers ratio)(Longhurst *et al.* 1952, Hornocker 1970, Seidensticker *et al.* 1973, Lindzey 1987).

Ratios for African lions can be difficult to calculate because much of their prey is migratory. If only resident prey are considered, Serengeti lions experience an overall predator-prey ratio of approximately 1:129 and a biomass ratio of 1:118 (calculated from data in Schaller 1972 and Van Orsdol *et al.* 1985). Ratios for individual prides are usually much higher. For example, Schaller's data for the Masai pride in the Serengeti show a predator-prey numbers ratio as high as 1:20. For my purposes, area-wide numbers are more useful.

Serengeti hyenas have a predator-prey numbers ratio of 1:86 and a biomass ratio of 1:266 (Kruuk 1972) (for consistency sake, Schaller's numbers for Serengeti prey were used for this calculation, but hyena numbers came from Kruuk). Considering lion and hyena together, total ratios are around 1:51 for numbers and 1:82 for biomass. But both of these ratios underestimate herbivore numbers and mass because they do not include migratory animals, which constitute over twice as much biomass as the resident herbivores (Schaller 1972). Since they are part of the system for only part of the year, their contribution is hard to estimate, but they are an important part of the diet for both predators and probably reduce the actual ratios by nearly one-half.

There is a higher density of both predators and prey in Ngorongoro than in Serengeti. Hyena densities, for instance, are about 14 times greater. Yet, using data in Kruuk, I estimate that the ratio of hyena (385) to prey (23,660) actually is 1:62 with a biomass ratio of 1:140. The relatively fewer lions (50) in Ngorongoro leads to a total (lion plus hyena) predator prey ratio of 1:54 and a biomass ratio of 1:97, nearly identical to those calculated for Serengeti. But considering the number and biomass of ungulates moving into Serengeti seasonally, predator:prey ratios in Ngorongoro truly are higher.

The above data suggest that the pristine ecosystems of late Pleistocene Beringia might reasonably be expected to have a predator-prey numbers ratio of at least 1:100, while the biomass ratio could be set conservatively at around 1:200, yielding an ecological efficiency of 0.05 %. The two ratios also imply that carnivores were consuming prey which was generally twice their own mass. Guthrie (1968) estimated Beringian predator:prey ratios from fossil frequencies and derived a numbers ratio of 1:130 for wolves and 1:250+ for lions, for a combined ratio of around 1:86. Even though there are numerous reasons to suspect preservational and collector biases against the smaller-bodied carnivores, Guthrie's ratios are very close to

my theoretical predictions. Using a ratio of 1:200, the herbivore biomass of eastern Beringia (1000 kg/km^2) would have supported approximately 5.0 kg of predators per km^2. Based on modern population dynamics and the fossil record, one might expect this biomass to be divided evenly between wolves and lions at 2.0 kg/km^2 each, leaving 1.0 kg/km^2 for other minor predators. This translates into 1 wolf every 25 km^2 (0.04 wolves/km^2; assuming a Pleistocene body size of 50 kg) and 1 lion every 100 km^2 (0.01 lions/km^2; assuming a Pleistocene body size of 200 kg).

These numbers are well in-line with modern demographics, and even suggest somewhat higher densities than present in the case of wolves. Of course the estimate is not very precise, and the 50-50 split between lion and wolf is only a best guess. The predicted lion density compares very well to densities of modern lions (average values around 0.01 - 0.08 according to Nowak 1991). The wolf estimate is exactly on order with the density of wolves in areas of Minnesota and Ontario, where they feed mostly on white-tailed deer in forest ecosystems (no parallel in ecosystem structure is implied)(Mech 1973, Van Ballenberghe *et al.* 1975, Fritts and Mech 1981, Fuller 1989). To expect such wolf densities in Pleistocene Beringia may be too optimistic, but the fact that Pleistocene wolves were smaller and may have been relegated to smaller prey items suggests that this estimate may not be too far off. It certainly is within the range of my conservative suggestion of 0.0033 wolves/km^2 and compares reasonably well with the density of wolves in modern Alaska.

Prediction for both wolf and lion densities based on predator:prey ratios suggest that my initial ballpark predictions (0.01 for wolves, 0.004 for lions) may have been too conservative. Alternatively, these levels of tertiary productivity suggest that the Pleistocene large carnivore guild may have been fairly rich, with significant numbers of scimitar cats, dholes, or cheetahs coexisting with lions and wolves. Either way, the implication to a population of scavenging short-faced bears is that there would have been many opportunities to confiscate carcasses from other carnivores, in addition to scavenging on herbivore carcasses resulting from natural mortality.

4. Relying on Carcasses as a Continuous Food Source and the Evolution of *Arctodus*' Scavenging Niche

Some authors have made the point that no large mammalian carnivore today is able to make a living by pure scavenging (see Houston 1979), and this is true — in modern ecosystems (vultures are the only large-bodied endotherm that does so today). In this section, I will be showing how a pure scavenging niche may be tenable for a large mammal under certain ecological and environmental conditions. I already demonstrated how it seems likely that North American ecosystems produced enough carcass

biomass annually during the Pleistocene to support scavenging short-faced bears. It is another question all together, however, whether that carrion would be available year-round and on a regular basis. If mortality among Pleistocene herbivores was highly seasonal, for instance, then short-faced bears would have faced seasons of huge dietary surpluses followed by long, lean periods and certain energetic bottlenecks. The following discussion will explore such issues, and in the process I will try to show that the key to *Arctodus*' extinction probably lies in changing patterns of carcass availability due to changes in herbivore demographics at the end of the Pleistocene. I will conclude by proposing a theory for the events which may have driven the evolution of a pure scavenging niche in *Arctodus*.

Feasibility of A Pure Scavenging Niche

I contend that there are two reasons why no large carnivore today subsists solely by scavenging. First, few ecosystems provide enough carrion biomass distributed evenly throughout the year. Second, no large carnivore living in such an ecosystem today is big enough to monopolize and defend carcass resources from its competitors. I address these reasons in order and explain how *Arctodus* may have overcome them.

Seasonal Carcass Abundance: The most critical tenet of the scavenging hypothesis may be the question of seasonal carcass abundance and whether carrion would have been a reliable year-round food source for *Arctodus*. While this is probably the most difficult aspect of the hypothesis to test, I believe light can be shed on the issue by re-examining aspects of the large herbivore populations in Pleistocene Beringia versus those of today. In my model of Beringian herbivore populations I followed Guthrie's (1982, 1984a, 1984b, 1990a, 1990b) rationale that Pleistocene herbivores were large-bodied and existed in low population densities. In the simplest terms, the reason for this pattern, according to Guthrie, is that Beringia's Pleistocene winter range supported fewer individuals of any given species and heavy winter mortality kept most populations of large herbivores understocked. Selection was for larger-bodied individuals which were able to take advantage of a longer and more productive growing season and invest conservatively in reproduction, often delaying reproduction for a season or two. Such an individual and its offspring would have increased fitness because they were more likely to survive subsequent winter bottlenecks in Pleistocene environments.

Guthrie emphasizes that this large-body strategy only applies to ruminants, not monogastric herbivores, because the latter have slow growth potentials and thus are not adapted to take advantages of seasonal spikes of high quality forage. As a result, Pleistocene monogastrics like horses and mammoths were not giants, but actually diminutive compared to their ruminant counterparts. However, since monogastrics are better adapted to using poor quality winter range, more of them may have been able to overwinter and thus summer productivity could be turned into more, but smaller, individuals

This sets up the following likely situation in Pleistocene Beringia: ruminants, dominated by bison, would have been in their worst condition and mortality rates would have been highest in late winter to early spring just before green-up. Carcasses of bison would have been plentiful for *Arctodus* at this time, but perhaps rare during other seasons. Today, mortality is highest in winter and spring among northern ungulates, including bison (Soper 1941, Kline and Olson 1960, Clutton-Brock *et al.* 1982, Ballard *et al.* 1981, Leader-Williams and Ricketts 1982, Berger and Cunningham 1994). In contrast, mortality amongst Beringia's horses and mammoths (the regions dominant monogastrics) should have been more evenly distributed throughout the year. Both proboscidian and equids have conservative growth strategies and live long lives (Klingel 1969, Janis 1976, Owen-Smith 1988, Haynes 1991), and rates of natural mortality in both are predicted to be low. Mortality in most populations of modern African elephants — a monogastric roughly analogous to mammoths— is not particularly seasonal, according to causes of death listed by Haynes (1991) and Owen-Smith (1988). Mass die-offs do occur in elephants and are related mostly to droughts (Hanks 1979, Owen-Smith 1988). They also occur most frequently in extremely arid areas such as in western Hwange Park, Zimbabwe, where it can be difficult for elephants to fulfil their requirement for daily water (Haynes 1991). Still, the earlier model showed how even low natural mortality rates in horse and mammoth alone could provide ample carcass biomass for short-faced bears — as long as it was evenly distributed throughout the year. Given Guthrie's demographic predictions, this seems plausible.

In stark contrast, the large herbivore guild of Holocene Beringia is composed exclusively of ruminants. In the most recent millennia, caribou and moose have dominated, but muskox, sheep, bison, and wapiti also have been members of the Holocene guild. All of these species experience highly seasonal mortality, and this factor, combined with low overall ungulate biomass leads to a situation whereby there are not enough carcasses available year-round to support an exclusive scavenger, much less such a large one.

Even wolverines, the carnivore most dependent on scavenging in this region, do not subsist completely on carrion (Rausch and Pearson 1972, Hornocker and Hash 1981, Magoun 1985, Gardner 1985). It is my impression that carcasses are a rare commodity overall in present day Beringia but that they can be a nutritional windfall at times to wolves, wolverines, and brown bears. If a carcass has been mutually located by any two of these carnivores, competition can be high, but there is a clear dominance hierarchy— bears dominate. Wolves will harass bears for access to a carcass, but they seldom prevail (Murie 1944, 1981, Ballard 1982, Magoun and Valkenburg 1996). Wolverines, while known for their ferocity, also are no match for brown bears (Murie 1981). Brown bears, wolves, and wolverines all will cache carrion presumably to prevent detection by other scavengers (Mysterud 1973; Murie 1981; Magoun 1976, 1985; Gardner 1985). This is understandable in wolves and wolverines, but there seems to be little

reason for brown bears to cache carcasses, since they normally remain near a carcass until it is consumed, as Murie's many anecdotes describe, and no other present-day carnivore can realistically steal a carcass from an attendant brown bear, except maybe a pack of wolves. Perhaps this behavior in brown bears is a reflection of past habits, when another, larger bear monopolized all carcasses unless they could be hidden from detection (especially by smell). A test of this hypothesis would be to examine whether brown bears in Eurasia habitually cache carcasses, since those populations have evolved in the absence of *Arctodus*. However, such data are unavailable.

I hypothesized earlier that no modern carnivore subsists totally by scavenging because few modern ecosystems provide enough carrion biomass distributed evenly throughout the year and because no large carnivore living in such an ecosystem is big enough to monopolize and defend carcass resources. Now I have presented reasons to suspect that Beringia's Pleistocene ecosystem may have been structured in a way such that carcasses were more evenly distributed throughout the year— mainly because of the former prominence of more monogastric herbivores.

The argument extends equally well to most of North America, which had even more monogastrics and other large herbivores with conservative growth strategies, including camellids, edentates, additional horse species, and another proboscidian (mastodons). In addition, western North America was occupied by a diverse group of antilocaprid species (Kurtén and Anderson 1980), which may fit well into the present *Arctodus* model, but for a different reason. Antilocaprids generally are small-bodied, which means they have a more rapid population turnover rate (higher rates of both mortality and fecundity) than larger ungulates (Eisenberg 1981, Hennemann 1983, Calder 1984, Owen-Smith 1988). The American pronghorn, the only extant antilocaprid, experiences fairly high mortality rates, even though it is moderately protected (Baker 1954, Folkner 1956, Fichter and Nelson 1962, Kitchen 1974). Baker (1954), for example, recorded a 10 % (non-hunting) winter mortality in 1952 for Wyoming pronghorn, while Hailey *et al.* (1966) reported on a Texas population that experienced a 30 % decrease in numbers in a single year. Twinning also is the norm in pronghorns, which adds to their rate of production (Chattin and Lassen 1950, Folkner 1956, Kitchen 1974).

A diversity of such antilocaprid species would collectively contribute more, but smaller, carcasses to the system on a more regular basis. These species still may have experienced a peak of seasonal mortality in the winter, as do modern pronghorn, but overall this pattern of high herbivore turnover would work well for an obligate scavenger, even a very large one, because such a scavenger does not need large carcasses so much as it needs a "large-enough" carcass at frequent intervals. A 50 kg pronghorn, for instance, represents about one week of food for *Arctodus*. Therefore, I predict that a system supporting an obligate scavenger will have one of the following two characteristics, or both. First, it will provide carcasses on a regular basis, which occurs when the system contains herbivores with conservative growth

patterns and herbivores that do not have marked seasonal mortality. Second, the system should have a fair number of smaller-bodied herbivores with rapid populational turnover rates.

Carcass Dominance and Carnivore Body Size: Having addressed the question of ecosystem structure, there still remains my second point about the scavenger's body size. In this regard, it seems that only bears, with their inherent large size, are preadapted to a niche of exclusive scavenging because only they are able to reach body sizes which allow them to monopolize carcasses. One could argue that big bears exist today in the Holarctic, yet none are exclusively scavengers. I would counter that Holarctic ecosystems today do not provide large amounts of carcass biomass throughout the year. Some modern temperate and tropical ecosystems probably do provide the necessary carcass biomass, but they do not have bears or any other carnivore large enough to monopolize carcasses, and I would argue that no other group of carnivores is big enough to cross that critical size threshold because they and their ancestors have come from the ranks of predatory carnivores. In Chapter 2, I showed how being a predator encumbers a species with certain morphological and size constraints, and that there is an upper size limit for mammalian predators because of locomotor demands involved with successful predatory tactics. From that standpoint, it is difficult to envision a group of predators evolving a large enough body size to then cross over to a mode of searching out, and, more importantly, defending carcases. There also are energetic barriers to overcome, as I have been discussing in the present chapter— namely larger predators need to capture larger prey or many smaller prey more frequently. Their bigger size makes the latter more difficult, and being dependent on larger prey means dependence on a food source that is inherently less abundant. All of these factors keep predators relatively small, making it difficult for them to evolve body sizes large enough to be dominant at carcasses.

In contrast, bears have evolved their large size as an integral part of their evolution away from pure carnivory and predation (Kurtén 1964, 1966b, 1967; Martin 1989; Stirling and Derocher 1990). Still, all bears retain a predisposition for carnivory. But their size and build makes them poor predators in all but the most opportune situations. At least one bear lineage — the brown bear-polar bear line— has secondarily increased its level of carnivory (Kurtén 1964), and this propensity seems to persist in the Ursidae. What is important to this discussion, however, is the ability of a bear to exploit its size for the purpose of dominating other carnivores. Bears today clearly are aggressive towards other carnivores (e.g., Rogers and Mech 1981, Ramsay and Stirling 1984, Miller 1985), and the original impetus for size evolution in bears during the Miocene seems best explained, at least in part, as a defense against predators, since bears could no longer outrun them.

A Theory for the Evolution of Scavenging in Short-Faced Bears

Given these dispositions in bears, I propose that short-faced bears diverged from a more generalized stock of forest-dwelling Tremarctine bears (around 1.5 - 2.0 Mya) as they increased their use of open habitats. Carrion is more easily located in non-forested environments (Schaller and Lowther 1969, Schaller 1972, Blumenschine 1989), so a critical factor in this evolution may have been the increased percentage of open savannahs and parklands in the western half of North America at the end of the Pliocene. Carcasses are difficult to find in forested environments and frequently they go undiscovered there presumably because they are hard to detect, as odors do not travel far and carcasses are difficult to spot in closed habitat (Craighead and Craighead 1972, Mysterud 1973). Therefore, it would seem unprofitable for a carnivore to focus its foraging efforts searching for carcasses in forests, and indeed, *Arctodus* fossils are associated with non-forested environments (Harington 1973, Kurtén and Anderson 1980, Harris 1985, Richards *et al.* 1996). In an open environment the scent of a carcass will carry farther and, once its direction is determined, visual detection is far easier than in a closed environment. Carcasses could be detected and found with little addition to a bear's normal foraging efforts. But this statement holds true for any carnivore in open terrain. What other carnivores lack, however, is size— enough size to dominate a carcass they find and monopolize carcass resources in general. Without this ability, it is hard to imagine how a carnivore could evolve a niche dependent on large mammal carcasses as its primary or exclusive food source.

Because of their size, bears are uniquely preadapted to evolve into a scavenging niche if the appropriate environmental conditions arise. Once a bear moves into such a niche and increases its dependence on carrion, and competition from other carnivores is keen, I would predict there to be selective pressures for even larger body size in order to ensure its dominance. But larger size has other key advantages for a scavenger. A larger animal can go longer between feeding bouts, and if it finds a large meal, it can eat more at one time (Houston 1979, Eisenberg 1981). These are ideal traits for a scavenger that depends on large carcasses for food— larger carcasses come from larger animals, which in turn have lower population densities and therefore will be less abundant.

Likewise, a larger animal has a lower cost of transport (previous paper) and thus can more efficiently cover a foraging area. Reciprocally, it can cover a larger area at a reduced cost. But such a strategy means the scavenger must find an absolutely greater amount of carrion to meet the energetic needs of a large body, even if it is metabolically more efficient. If such a large-bodied scavenger begins to focus primarily or exclusively on large carcasses for food, then selection should favor morphological changes that increase locomotor efficiency even further. These would include a reduced musculoskeletal mass, increased leg (stride) length, cursorial limb posture, and an economical gait for moderate speed travel— traits which all are found in *Arctodus*.

But why did *Arctodus* evolve such a huge size? Those who subscribe to predatory models have used *Arctodus*' size as an indication of its prey size— in other words, as a reflection of herbivores in the mammal community. Under the scavenging model, *Arctodus*' size becomes a reflection of other carnivores in the community — that is, it is an indicator of the level of aggression, and perhaps the degree of sociality in Pleistocene carnivores. If *Arctodus* only needed to defend carcasses against a few wolves or a lion or two, then it is hard to see why it had evolved to be so large. Even the energetic reasons I have discussed do not seem reason enough to explain its size. Given corroborating evidence, I think it is reasonable to conclude that *Arctodus*'s size is an indicator of high levels of competition amongst carnivores and that *Arctodus* was defending itself and its resources against groups of social carnivores which had a large cumulative biomass (i.e., group size need not have been large if individuals were large-bodied).

Today clear examples can be found of competition driving the size of carnivore social units as well as body size. Lions and spotted hyenas are classic examples. Two female lions (weighing about 150 kg each) can keep 5 - 6 spotted hyenas (weighing about 50 - 60 kg each) from stealing their kills, but the mere presence of a male lion (weighing 200 - 250 kg) can keep up to 12 hyenas at bay (Eaton 1979). Indeed, the large size of male lions is believed to have evolved in part because of their role in defending kills and prides against the smaller, but highly social hyena (Kruuk 1972, Schaller 1972, Eaton 1979). (Male lion size also appears to be driven by male-male competition as coalitions of males vie for control of prides (Packer *et al.* 1988)). Even a small pride of female lions is nearly invincible to hyenas with a male present. Competitive dynamics of body size and group size also play out in interactions between these two dominant carnivores and hunting dogs, leopards, and cheetahs. The solitary nature of leopards and cheetahs ranks them very low in their competitive abilities, but the large packs of the highly social African hunting dog make them nearly equal competitors to the larger-bodied hyena (Estes and Goddard 1967; Kruuk and Turner 1967; Kruuk 1972; Lamprecht 1978, 1981; Eaton 1979).

Earlier I summarized arguments showing why Pleistocene lions probably existed in very small groups and most likely did not form typical prides, at least in Beringia. But still, two or three large lions constitute quite a threat to any mammal, even to a 700 kg short-faced bear. This is especially true considering the revised carnivore body mass estimates of Anyonge (1993); according to Anyonge, Pleistocene lions weighed 344 - 523 kg. Previous estimates have placed them about 1 ½ times the size of modern lions, in the range of 200 - 375 kg (Anderson 1984, Stock and Harris 1992). In Chapter 2, I tried to show that body size severely limits predatory abilities in carnivores over about 250 kg. If this analysis is correct, then Anyonge's estimates are hard to believe, since a 523 kg lion would have been an inept predator. Using either either of the above estimates of lion body size, the presence of lions in North America seems like a compelling force driving increased body size evolution in *Arctodus*.

Other felids in North America almost certainly were not social, with the possible exception of sabertooths. The modern decedents of Pleistocene cheetahs, and their closest other relative, the puma, all are quite solitary (with a few exceptions), suggesting *Miracinonyx* was as well. Jaguars, which inhabited western North America during warmer intervals of the Pleistocene are not social cats either. Traditionally, it has been argued that Smilodine and Homotherine sabertooths probably did not form prides, mainly because a solitary lifestyle is the rule for felids, with lions being the only exception. Radinsky (1975) and Hemmer (1978) argued further that sabertooths were non-social based on brain size and morphology. Turner (1997) questions the validity of comparing brain size, even when scaled to body size, because accurate estimates of body size do not exist for the morphologically-unique sabertooths. Turner (citing Graham 1976) further argues that the high occurrence of *Homotherium* deciduous teeth and juvenile mammoth remains at Friesenhahn Cave provides circumstantial evidence that these cats may have hunted young proboscidians, and Turner believes this would have been inconceivable for a predator the size of *Homotherium* unless it hunted in groups. The high incidence of bone lesions found on *Smilodon* fossils at Rancho La Brea, and the case of a sabertooth canine being lodged in the skull of another sabertooth, have been cited as evidence that sabertooths were aggressive towards each other and generally asocial (summarized in Turner 1997). But Shaw *et al.* (1991) and Heald (1989) have interpreted healed wounds in *Smilodon* as a sign that this sabertooth was social because it is difficult to see how an injured sabertooth with bone pathologies could survive unless it had access to kills made by pride-mates.

In groups, or alone, sabertooths probably were formidable competitors in Pleistocene North America, and Anyonge's (1993) latest estimates for body mass are 146 - 231 kg in *Homotherium* and an amazing 347 - 442 kg in *Smilodon*. Marean and Ehrhardt (1995) argue that *Homotherium* was capable of disarticulating large mammal carcasses, but this is questionable due to the extreme specialization of sabertooth dentition for killing and cutting at the cost of bone processing abilities (Ewer 1967,1973; Blumenschine 1987, 1989; Marean 1989). Either way, sabertooths were the least adapted of all large carnivores for processing carcasses to their fullest, and it is likely they left considerable edible material on the bodies of animals they killed (Schaller and Lowther 1969; Ewer 1967, 1973). Sabertooth kills thus would have been a real boon for a scavenger with abilities to process carcasses more thoroughly— an idea which has been proposed for hominid scavengers as well (Schaller and Lowther 1969; Marean 1989; Blumenschine 1986, 1987, 1988).

Potential canid competitors of *Arctodus* included wolves, dire wolves, and perhaps coyotes (*Canis latrans*). Modern coyotes depend on carcasses from other predators' kills perhaps more than any other large canid (Young 1951) and coyotes will form temporary associations at carcasses to defend them (Bueler 1973, Bekoff and Wells 1986). Coyotes also have an occasional tendency to form cohesive social groups when hunting cooperatively for large prey in areas where coyotes and wolves are not sympatric

(Bowen 1981). Coyotes were larger in the Pleistocene (Nowak 1979), but given the tendency of coyotes to be subordinate to larger canids (namely wolves), the presence of two other (social?) canids in Pleistocene North America suggests that Pleistocene coyotes were solitary.

There is no disagreement that Pleistocene wolves were social, but it is difficult to estimate their pack size. Wolves today can form large packs, sometimes upwards of 15 to 20 individuals, but this is rare (Rausch 1967, Mech 1970, Haynes 1982). Also, the mechanisms driving pack size remain elusive (Rausch 1967, Pimlott *et al.* 1969, Mech 1970, Rodman 1981, Pulliam and Caraco 1984, Earle 1987). There is some evidence that wolves form larger packs in situations where they frequently lose carcasses to grizzlies (Ballard 1982), but the prevailing theories implicate prey size and prey density as the determinants of pack size: packs that hunt larger prey and/or prey with low-densities have more individuals (Murie 1944, Burkholder 1959, Rodman 1981, Oosenbrug and Carbyn 1982, Pulliam and Caraco 1984, Earle 1987). Body size in wolves is only loosely associated with prey size, and it seems that the strategy of wolves is to match pack size rather than body size to prey size. Pleistocene wolves were slightly smaller than today (Matheus 1998), but for the reason just stated, this may not have reflected prey size. Instead, it may suggest that packs were larger, since a pack of given total mass can be composed of many small individuals or few large individuals.

In this regard, Pleistocene wolves may have hunted more like the smaller African hunting dog of today, which specializes on small to moderate-size bovids by hunting in large packs— averaging around 7 - 11 individuals (Kruuk 1972, Bertram 1979). Hunting dogs can kill animals as large as adult wildebeest (at least 5 - 7 times their own size), but their small size excludes them from hunting the very largest African bovids. The hunting dog's forte is using its speed and large numbers to chase down swift bovids, mainly gazelles, which they capture when the gazelle makes a sharp evasive turn and runs into a well-positioned pack member (Kruuk and Turner 1967). Hunting success rates are high in hunting dogs, but they must hunt often because each kill must feed many individuals, and because their prey is relatively small-bodied. If Pleistocene wolves were hunting this way, it would explain how prey resources were partitioned between them and lions, which because of their size must have been focusing on much larger-bodied prey. The large pack size of hunting dogs also makes them rank on par with the larger spotted hyena for access to carcasses (Eaton 1979). The same could be said for a pack of small Pleistocene wolves trying to defend carcasses from lions or short-faced bears. Also, the prediction that these small wolves killed smaller prey, but more frequently, compliments *Arctodus*' niche, as presented in this paper, because it would increase the average number of carcasses on the landscape at any given time.

There is no direct evidence of pack size in dire wolves, but their exceptionally high numbers at Rancho La Brea— where they are more abundant than any other species— has been interpreted as an indication that they formed large packs (Stock and Harris 1992). Compared to grey wolves, the dire wolf

was slightly larger and more heavily built in both its limbs and cranium. Its canines and carnassials were larger, too, and the latter were highly sectorial. Because of its robust build and dentition, it has often been suggested that the dire wolf may have done substantial amounts of scavenging (Kurtén and Anderson 1980, Stock and Harris 1992, Van Valkenburgh 1989), but I find little logic in this. First, the canines of the dire wolf were long and compressed, an adaptation for piercing and killing (Van Valkenburgh and Ruff 1987). While its larger premolars would function better as bone crackers, bone-cracking does not necessarily signify a scavenging lifestyle, so much as it indicates the degree to which a carcass is utilized. As I have tried to show in this chapter, an argument for scavenging requires one to demonstrate that the whole animal has evolved to maximize its access and ability to utilize carrion resources, often at the expense of predatory skills. Yet, the number of traits in dire wolves that point to a predatory lifestyle are equally great, such as canine size and shape. Moreover, all predators will engage in scavenging behavior when the opportunity arises, so to speculate on whether an extinct predator scavenged, or to what degree, can be pointless. Of course, this is different than building the argument that a species evolved specifically within a scavenging niche.

If any of these predators faced a constant threat of losing their prey to an exceptionally large, carcass-stealing specialist, as I have proposed, then there would have been clear impetus to increase body size and/or pack size for defense. Lions displayed large body size, as did dire wolves. Both may have had only small social units, but their size and strength may have made them competitive with short-faced bears even in small numbers. Wolves apparently took a different route in this competitive scheme. They were smaller-bodied, but they likely formed larger packs than today. In response to this competition, selection in *Arctodus* would have been for even larger size, as long its scavenging niche remained energetically tenable (later, I will discuss how this tenability may have been lost).

In the previous paper, I noted that *Arctodus*' inflected pelvis, short hind limbs, and short back were well suited for a bear that used an upright stance. In context of the current discussion, I would argue that this behavior would be a valuable in an animal that intimidated other aggressive and social carnivores either for defending a carcass or for stealing one. If a scavenger wants to ensure its control over a carcass, it must make an unmistakable presentation to other carnivores that clearly states its dominance, and size is the clearest indicator. Larger social groups of competitors require the impression of even larger size, and an upright stance has the effect of greatly increasing an animal's apparent size, especially during a frontal display. I estimate that when the average *Arctodus* stood upright it would have been about 2.5 m tall at head height. Harington (1996) and Voorhies and Corner (1982) estimate that the largest short-faced

bears would have stood 3.4 m tall, with a vertical reach of 4.3 m![3] As with the propensity for large size, being able to stand upright in an intimidating posture is a trait uniquely available to bears, as no other carnivore can realistically stand bipedally. But an upright stance is not the standard aggressive posture or threat display of Ursine bears. However, Hererra *et al.* (1991: 67) note how spectacled bears, the only surviving Tremarctine bear and *Arctodus*' closest living relative, have a reputation amongst local people for chasing humans while standing upright. They state: "... bears will chase people away and are very dangerous when they get up on their hind legs."

Elsewhere (Matheus 1995), I have noted that *Arctodus*' cranial and dental morphology also supports the scavenging hypothesis (also see comments in Voorhies and Corner 1985, Guthrie 1988, Baryshnikov *et al.* 1994). Its massive jaw musculature and shortened outlevers of its teeth would have yielded a very strong bite force, and its carnassials, which were ill-adapted for sectorial action, would have been positioned well to function as bone-cracking hammers (Matheus 1995). Such a suggestion can almost be taken for blasphemy amongst mammalogists, but Van Valkenburgh (1996) recently showed that African large carnivores display considerable "slop" in the use of their teeth for prescribed functions, and indeed she records the regular use of carnassials as bone cracking devises in spotted hyenas and hunting dogs (also see Sutcliffe 1970).

Such features of the skull in *Arctodus* are indicative of a carnivore that had the ability to open and process large mammal carcasses, and I disagree with Kurtén (1967) that the skull is adaptive in any significant way for predation. Kurtén argues, for instance, that *Arctodus*' wide palate was adaptive for "worrying prey," but this trait may just be coincident with a wide snout that was used to smell-out carcasses over a large area. Standing alone, neither proposal is more or less reasonable than the other, but the latter fits more congruously with other data on *Arctodus*. Likewise, *Arctodus*' canines do not suggest any adaptation for predation, such as lateral compression (using criteria of Van Valkenburgh and Ruff 1987). Instead, they are round and generic like those of other bears, only larger. Speculating on the role of *Arctodus* as a flaker of Pleistocene bone, Voorhies and Corner (1986) seem to imply that short-faced bears could have used their canines to break bones, and Guthrie (1988) comments on the ability of brown bears to puncture steal with their canines. Larger canines may have evolved in *Arctodus* from this selective pressure, but it seems unlikely to me. Amongst other more likely alternatives is the possibility that *Arctodus*' canines were used agonistically against other short-faced bears. Indeed, the degree of sexual dimorphism in canine length is correlated to breeding systems (e.g., monogamy, polygyny) in Carnivora, not diet (Gittleman and van Valkenburgh 1997). I did not examine the degree of canine sexual

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[3] My estimate of bipedal height is based on the length of the hind legs (femur and tibia) plus the length of the spine and the height of the skull. Using data from Table 8 in the previous chapter, these lengths total 2.5 m. It is unclear how the other authors cited derived such large estimates.

dimorphism in short-faced bears, but this question should be pursued as a possible clue into *Arctodus'* breeding biology.

Furthermore, if *Arctodus* had evolved as a predator, there should be a greater dissimilarity between its teeth and those of other bears. For instance, during its short evolution, the highly predatory polar bear has developed teeth that are clearly distinct from those of brown bears, its direct ancestor. Polar bear teeth are smaller, higher crowned, narrower, and more trenchant, than brown bear teeth giving polar bear teeth more sectorial qualities. Over its 1.5 to 2.0 million year history, *Arctodus* never developed comparable traits. Kurtén (1967) argued that the protocone of *Arctodus'* P^4 was positioned more posteriorly, giving this cusp a blade-like quality (Stock and Harris 1992 concur). I have examined most of the *Arctodus* dentitions in existence and do not see this trait in the P^4. Therefore, I can not agree with the conclusion of these authors. Instead, I find that there is high variability in the position of the protocone both in *Arctodus* and other bears (except polar bears), and, if anything, the P^4 has a broader and more pyramidal shape in *Arctodus*. As I mentioned, this tooth would function best as a bone cracker, and it typically has a fairly flat anterior-posterior wear-facet inclined lingually about 20°, a pattern similar to that found on premolars of spotted hyenas. Given the fact that the remainder of *Arctodus'* cheek teeth remained so "bear-like," it seems most congruous to argue that they retained their function as crushing apparatuses. This configuration would suit a carcass-processing animal well because such an animal could use its broad posterior molars to crush smaller bone and it could fracture large cortical bone using the apex of its P^4 and the triconid of the M_1 as cracking hammers. It is even possible, but as yet untested, that *Arctodus* had evolved the ability to digest bone as modern hyenas have. Energetically, osteophagy extends the feasibility of the scavenging niche, and perhaps is a key component of it (Martin and Martin 1993).

Earlier, I made the point that simple one-to-one comparisons between *Arctodus* and other carnivores would lead to spurious conclusions, and that a first-principles approach is more appropriate. The former approach led Baryshnikov *et al.* (1994: 350) to conclude that, "*Arctodus simus* was not as highly specialized a scavenger as *Crocuta* or *Canis dirus*. Their carnassials lay [too far] forward, to be effective. *Crocuta* can 'cut' and 'crush' bones... . *Arctodus* simus could less effectively crush small bones; big bones of mammoths were probably not accessible for *Arctodus*." (secondary quotes are mine). I find these conclusions puzzling because they do not agree with the morphology of *Arctodus*, and to expect such a strict morphological recipe for bone processors is unreasonable. Moreover, *Crocuta* appears to have evolved as an osteophagous predator, and the carnassials are not the fundamental tooth used by *Crocuta*, or any other modern carnivore to process bone (Sutcliffe 1970; Ewer 1967, 1970; Kruuk 1972; Van Valkenburg 1989, 1996). Also, hyenas do not "cut" bone, they crack and crush it. Bone "cracking," as opposed to "crushing," is a process by which strong biting forces are transmitted usually to a single, well-backed apex on a tooth so that these forces are focused on a narrow point of the bone. This initiates a

fracture in the crystalline bone matrix. When the wider basal portion of the tooth is driven into the bone, this expands the fracture and causes it to propagate as a long crack. Any tooth of the proper configuration and position in the tooth row can be employed for such a function (as long as the action does not generate so much torque as to dislocate the jaw, which is more likely with more posterior teeth because they have shorter outlevers). In contrast, "crushing" occurs when one solid object obliterates the structural integrity of another softer and less dense object. There is less need when crushing bone to focus the biting force in a single apex, in which case broad, flat teeth which are close to the jaw articulation suffice.

Baryshnikov *et al.*'s (1994) contention that *Arctodus*' carnassials were too far forward to process bone, also is difficult to accept. If these authors were looking for analogous structures in *Crocuta*, they should have compared *Arctodus*' carnassial to *Crocuta*'s P^3 and P_4, which are conical-shaped and the primary teeth used by *Crocuta* to crack bone. Also, the forward position of *Arctodus*' carnassials in the tooth row is less significant than the fact that the face was shortened overall, which brought the carnassials closer to the jaw articulation and gave them increased mechanical advantage. Finally, Baryshnikov *et al.*'s statement that "*Arctodus simus* could less effectively crush small bones" seems to go against reason. A bear that large and with such a powerful masticatory anatomy would have no problem crushing small bones, as discussed above. Even the much smaller wolverine can crush and crack large mammal long bones (Krot 1959, Haglund 1966, Magoun and Valkenburg 1996).

Extinction

Throughout these chapters I alluded to two possible contributing factors in *Arctodus* extinction, all relating to its huge size. Here I will briefly summarize them in the form of two hypotheses.

1) When discussing home range size and population densities, I suggested that *Arctodus* faced a fundamental conflict due to its size: how does such a large-bodied carnivore exist in population densities low enough so that each individual has a large enough exclusive foraging area, yet still retain a minimal viable population size? The first tenet of this question is an energetic one relating to the prediction that a carnivore the size of *Arctodus* must forage over a tremendous home range just to find enough food to meet its energetic requirements. Indeed, this is why I argued that *Arctodus* was built for increased locomotor efficiency. But it is conceivable that large mammal carcasses became so widely scattered that each bear would have to forage over an increasingly larger area, to the point where the environment supported a population density so low that the species fell victim to inevitable chance extinction. This process would have been amplified by the likelihood that home range overlap decreased as densities dropped, leading to populations that were further fragmented, whereby the chance of random extinction increased further.

Stated in another way, decreasing carcass densities would have increased the size of individual foraging areas to a point where each bear would have had to travel so far to find carcasses that it became

impossible to balance its energetic budget between foraging costs and foraging gains. This may have even become a limiting factor before population sizes fell below minimum levels required for reproduction.

2) Rather than a reduction in absolute carcass production, the most important factor in *Arctodus*' extinction may have been a change in the regime or carcass abundance— namely, from a Pleistocene regime, characterized by weakly seasonal carcass availability, to a Holocene regime, characterized by strongly seasonal carcass availability. In my modeling, I suggested that increased herbivore diversity during the Pleistocene and the presence of monogastric herbivores with more conservative growth strategies (i.e., equids, proboscidians, and other non-ruminants) would have made carcasses readily available year-round in Beringia and the rest of North America. The abundance of small ungulates with rapid turnover rates also would have produced more carcasses more consistently. In contrast, Holocene ecosystems are marked by seasonal spikes of carcass availability because of reduced herbivore diversity and the predominance of ruminants. Today, carcass spikes are a nutritional windfall for northern carnivores, but none can make a living completely from carrion.

Regardless of the proximal cause for its extinction, it must have been *Arctodus*' huge size that ultimately brought on its demise. An obligate carnivore the size of *Arctodus* would have required such a large mass of flesh at regular intervals that, despite its energy-conserving design, this bear's annual energetic budget could not be balanced in Holocene ecosystems of North America. Those large carnivores that did survive Pleistocene extinctions are antitheses to *Arctodus*. Wolves switch types and size of prey and even forage on vegetation, and their foraging unit— the pack— has a flexible "body size" that changes seasonally. Brown bears are the hallmark of dietary and ecological plasticity; they have the behavioral flexibility *Arctodus* probably lacked, and, perhaps most important, brown bears do not need to eat for more than half the year because they hibernate. It is not known whether short-faced bears could hibernate, but I have suggested that it was unlikely (Matheus 1995). In some ways, wolverines are like miniature short-faced bears in that they are the most focused of all extant carnivores on carrion resources. Yet, like the wolf, they do not require large amounts of meat year-round. Most important, however, is their size— because they are so small, wolverines can get significant energy from both small and large carcasses. *Arctodus*' size made it dependent on larger food items. The wolverine also is a capable predator, able to find it profitable to hunt prey in a variety of sizes, from ground squirrels to caribou. While I will not claim that *Arctodus* never killed any of its food, these last three chapters have been devoted to making the point that it was not an adept predator. And unlike the wolverine, if *Arctodus* was a predator, its size dictates that it could not have gained any energetic benefit from hunting prey the size of a ground squirrel. Puma are the only solitary obligate large predators extant in northern North America, but their persistence also may relate mostly to their size. Like the wolf, they are able to use large and small prey items and can switch prey seasonally. The puma's ability to use a variety of broken terrain, from

dense forest to badlands, gives it a flexibility *Arctodus* may have lacked, since it needed to be in environments where it could detect carrion. Indeed, *Arctodus*' distribution indicates that it had a strong preference for open terrain (Harington 1973, Kurtén and Anderson 1980, Harris 1985).

In closing, I submit that if short-faced bears were predatory, and had a penchant for larger prey, then they should have persisted into the Holocene as hunters of the great bison herds inhabiting central North America. Of all late Quaternary carnivores, *Arctodus* would have been best able to follow the bison herds because of its size and ability to travel long distances efficiently. Alas, *Arctodus*' inability to catch and kill bison meant it could not follow such a strategy. Today, wolves follow caribou herds in northern Alaska and Canada (Kuyt 1972, Stephenson and James 1982) but they do not wait for caribou to die, or for another predator to kill them. Instead, the wolf is built to both follow the caribou and to kill it. *Arctodus* was not.

CHAPTER V

PLEISTOCENE CARNIVORES AND HUMANS IN EASTERN BERINGIA: DID SHORT-FACED BEARS REALLY KEEP PEOPLE OUT OF NORTH AMERICA? [1]

ABSTRACT

*Val Geist has hypothesized that the presence of short-faced bears (*Arctodus simus*) in eastern Beringia, along with other more aggressive Rancholabrean carnivores, may have been the critical factor excluding humans from North America prior to the last few thousand years of the Pleistocene. Predictions and assumptions of Geist's hypothesis are tested by: 1) re-evaluating the fossil record of large carnivores in North America vs. Eurasia, 2) integrating new data on* Arctodus *' ecology and behavior, and 3) using new radiocarbon dates on* Arctodus *to compare the chronologies of humans and short-faced bears in Beringia. This re-analysis leads to the conclusion that overall aggression from large carnivores was no greater in North America than Eurasia, except I agree that the presence of the extremely large and aggressive short-faced bear does stand out as a unique feature of Pleistocene faunas in North America. New stable isotope data and morphological considerations advance the hypothesis that* Arctodus *was a specialized scavenger, and that this would have made the bear even more dangerous to humans than if it was predatory. Nonetheless, Geist 's hypothesis is still rejected because radiocarbon dates on* Arctodus *suggest that it may not have survived later than 20,000 B.P. in Beringia, even though terminal dates are around 11,500 B.P. south of Beringia. This timing means that* Arctodus *may have been extinct in Alaska up to 8,000 years before Asians were even poised to cross the Bering Land Bridge.*

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INTRODUCTION

In two recent papers, Val Geist (1989, 1994) presented arguments for his hypothesis that aggressive large carnivores in Pleistocene North America, especially the giant short-faced bear (*Arctodus simus*), prevented Asians from crossing the Bering Land Bridge and gaining an permanent foothold in eastern Beringia prior to around 12,000 B.P. According to Geist, North America's large predator species were larger and more aggressive than in the Old World, and humans had limited technologies for dealing with this threat— a threat spearheaded by this super-huge bear, the likes of which people had never known (Fig. 25). Only with the extinction of these super-predators at the end of the Pleistocene could humans safely enter North America. This lively hypothesis has gone largely unacknowledged by anthropologists concerned with the peopling of the New World, perhaps because it seems largely speculative and untestable. But Geist presented very compelling arguments and strong inferential data in support of his hypothesis that should force us to seriously consider it.

In this paper, I examine the biological assumptions and fossil data upon which Geist's hypothesis rests, and I present new information about *Arctodus*, including behavioral, ecological, and chronological data that will help us more accurately infer the potential interactions between humans and short-faced bears in late Pleistocene Beringia. The new data show that while Geist's hypothesis is biologically sound, the fossil record does not unequivocally support his notions about Pleistocene carnivores. More important, there is a large chronological gap between the apparent timing of *Arctodus*' extinction in Beringia and the time that Asians were poised to enter Alaska.

SUMMARY OF GEIST'S HYPOTHESIS

First, I want to present a general overview of the main premises, and often eloquent arguments, of Geist's hypothesis. In the next section I will take a closer look at the assumptions behind Geist's hypothesis and re-examine the fossil evidence.

In order to follow Geist's arguments, it is important to understand his vision of Pleistocene North America. Geist proposes that North America's Rancholabrean large mammal fauna was characterized by an intense co-evolutionary predator-prey regime. Compared to late Pleistocene faunas in the Palearctic, Geist argued that North American ungulates were bigger and developed more elaborate horns and antlers (antipredator devices) in response to the types of predators in North America, which he contended were more numerous, larger bodied, and more aggressive. He also argued that both ungulate and carnivore diversity, and thus competition, were higher in North American. Essentially, Geist portrays North America's predators and ungulates as being engaged in a coevolutionary arms race. As evidence for this

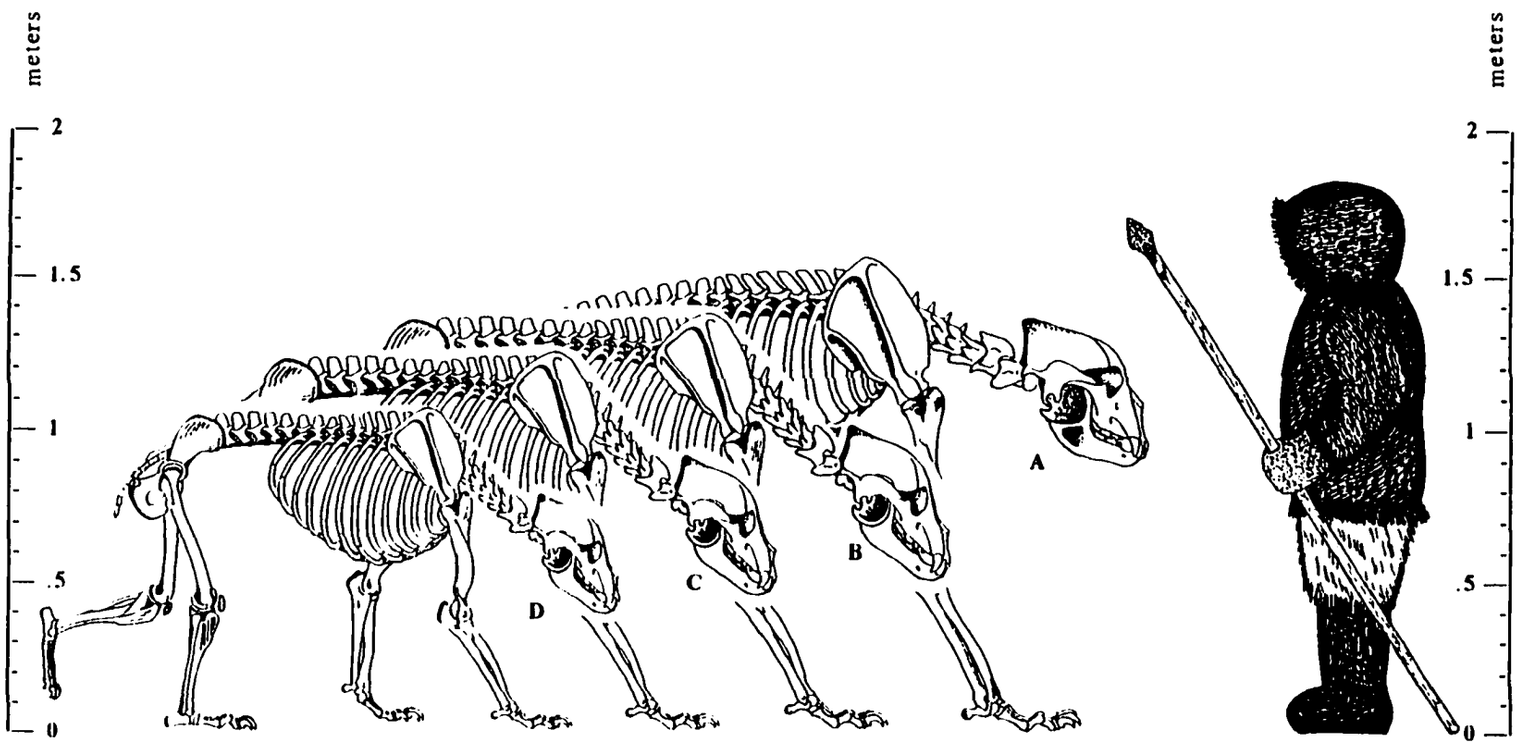

Figure 25. Size comparison of short-faced bears and brown bears. A) large male short-faced bear, B) largest size attained by coastal brown bears of today (could also represent the largest polar bear), C) large male brown bears typical of eastern Beringia during the late Pleistocene (also approximate size of a large modern, coastal brown bear), and, D) large male grizzly from modern interior Alaska. (original illustrations by author)

model, he contended that not only were fossils of late Pleistocene ungulates in North America larger than conspecifics in Europe or Asia, but that when Eurasian species migrated to the New World they quickly evolved larger body sizes and enlarged horns/antlers in response to competition. As examples of this pattern, he cited the morphological changes observed in *Bison*, *Ovis*, and *Cervalces* after they migrated from Eurasia to North America in the mid-Pleistocene. Thus, Geist uses the morphology of North American ungulates as indicators of an intensified predatory regime.

In Geist's opinion, North America's highly co-evolved Rancholabrean fauna (which, in his strict terminology, generally excludes eastern Beringia) was composed primarily of ecological specialists. The adjacent Siberian fauna, from which a considerable number of North America's modern mammals are derived, was composed of species that were relatively less specialized. In eastern Beringia, the two faunas mixed. According to Geist, it was difficult for Siberian generalists to make inroads into North American ecosystems, and the only successful ones were those that adapted to the intense predatory regime via increased body and/or horn size, as in the case of herbivores like *Bison*, *Ovis*, and *Cervalces*, and carnivores, such as the lion (*Panthera leo atrox*).

Eastern Beringia (unglaciated Alaska and the Yukon Territory) is a pivotal region in Geist's model. During the late Pleistocene, its mammalian fauna was, in a sense, a mix of Siberian and Rancholabrean species, but the picture is not quite that simple. About half the species in eastern Beringia also inhabited portions of the rest of North America, particularly the northern great plains and the West. However, it is important to note that many typical Rancholabrean mammals of North America did not extend their ranges north into Beringia. On the other hand, the vast majority of east Beringian mammals also lived in western Beringia (northeast Siberia), and very few species found in western Beringia did not also inhabit eastern Beringia. Only a handful of "Siberian" species in Alaska and the Yukon were able to colonize farther south into the rest of North America and contribute significantly to Rancholabrean communities (e.g., *Panthera*, *Oreamnos*, and *Vulpes* during the Illinoisan/ Sangamonian, *Bison*, *Ovibos*, and *Bootherium* earlier). This is an important point in Geist's predation hypothesis, because he argued that Rancholabrean specialists and super-predators formed an ecological barrier to the spread of "ill-adapted" Siberian mammals— including humans. In the closing millennia of the Pleistocene, Rancholabrean ecosystems began to collapse, culminating in the extinction of many large mammals, including its super-predators and super-competitors. Only then, Geist contended, could humans and other Siberian species bottled up in Beringia spread south into the rest of North America.

According to Geist, humans were poised in northeastern Asia and ready to enter North America in mid-Wisconsinan times (later, I discuss how most evidence is to the contrary), and he used largely discredited evidence (interstadial artifacts in the Old Crow region, Yukon Territory) to suggest that humans even made a few early forays into the continent. But Geist contended that these early occupations

ultimately were untenable in the presence of super-aggressive Rancholabrean large predators, especially the putative king of super-predators— the giant short-faced bear. He further argued that in the super-competitive and super-predatory world of Rancholabrean communities there was no room for an additional predator of large game, particularly a small bipedal one equipped only with light weapons. Indeed, late Paleolithic weapons were almost universally designed to kill small, thin-skinned game at long range (Guthrie 1983). On top of that, Geist suggested that the predatory pressure of Rancholabrean North America would have turned human hunters into prey. To this effect, Geist (1994) made the following statement that summarizes his position about the role of *Arctodus* in human expansion into the New World:

> *"Perhaps only with the disappearance of the short-faced bear humankind's single most ferocious predator— could New World hunters live off ungulates like the proverbial mice in cheese."*

Geist further presented compelling evidence that throughout pre-firearm history, humans have had difficultly contending with large, aggressive predators, particularly bears. According to his theory, brown bears approach an upper limit in terms of predator size and aggression that human hunters can safely deal with either while hunting bears directly, or while defending themselves and their possessions. According to Geist, even large bodied subspecies of brown bears and polar bears probably exceed safe limits (without the use of dogs), and short-faced bears far surpassed them. Furthermore, special weaponry is needed to hunt bears, including bear lances with extraordinarily stout and long shafts tipped with broad, sturdy points. But there is no evidence for these types of weapons in the late Paleolithic on either side of Beringia. Even with lances, bear hunting and defending oneself against bears still is a risky business— too risky if the bear is larger than an average grizzly bear (around 300 kg). Escaping bears by climbing trees was not an option, either, on Beringia's treeless landscape. So, Geist argued that if short-faced bears were the dominant aggressive predator in North American ecosystems (an assumption I shall address later), then they would have been too great of a threat to humans, both directly in the form of predatory aggression, and indirectly in the form of competition for game and robbing meat caches. Expanding populations of late paleolithic hunters in northeastern Asia had no means to protect themselves from predation by short-faced bears, and when hunters killed game they did not have adequate means to protect this resource from North America's "single most ferocious predator."

Assumptions Behind Geist's Hypothesis and the Fossil Record

Geist placed considerable emphasis on the differences between Rancholabrean and Siberian faunas, arguing that most Siberian mammals were excluded from North America by the latter's more aggressive and more competitive large mammal community. However, it seems that Beringia's biotic history, especially the faunal connections between Siberia and North America, is better explained by the coupled effects of sea level changes and the size of the Laurentide and Cordilleran Glaciers, not competitive exclusion. During glacial maxima, lower sea level meant that east and west Beringia had a dry connection via the Bering Land Bridge, but at the same time the Laurentide and Cordilleran ice masses were coalesced over most of Canada, effectively blocking passage between eastern Beringia and the rest of North America (Guthrie 1990a, 1990b). Therefore, during glacial maxima, Siberian species were able to enter Alaska and western Yukon Territory, but could proceed no further into North America. During periods of climatic amelioration, glaciers retreated and an ice-free corridor re-connected eastern Beringia with areas to the south. However, most Siberian species did not spread south because they were essentially adapted to cold, arid environments of the north, and many of their ranges probably contracted back to more arid regions of northeast Asia. On the other hand, during interglacials and interstadials, Rancholabrean species would have been able to expand north— both because of the open corridor (retreated glaciers) and because of the return of more temperate, mesic conditions there, to which these species were adapted. During these warmer/wetter phases, however, sea levels were high enough to inundate the Bering Land Bridge and prevent Rancholabrean species from entering Siberia via Alaska. So, it would seem that the distribution of Siberian and Rancholabrean mammals can be explained just as effectively using well established data on paleogeography, without invoking competition and predation.

Next, I want to re-examine the evidence for Geist's inferences about the differences between Nearctic and Palearctic carnivores. It was Geist's contention that more intense predatory pressure in North America led to larger body size and horn size in ungulates there, and that in this co-evolutionary battle there was selective pressure for North American predators to became even larger and more aggressive. Geist also argued that there simply were more species of large predators in Pleistocene North America during the mid-to-late Pleistocene. While there were obvious differences in the identity and nature of large predators in North America and Eurasia, I will argue that these differences reflect distinct biogeographic legacies, and I will challenge the notion that there were significant differences in the body size, diversity, and aggression of predators in these regions.

Intuitively, the biological premise of Geist's ideas seems sound, as somewhat parallel examples can be found today. For instance, the evolution of ungulates in southern and eastern Africa appears to be

strongly tied to predatory pressures. Morphologically and behaviorally, these ungulates invest considerable resources into avoiding predation, and it can be said that because of their long period of coexistence they are approaching a theoretical form of coevolutionary equilibrium (Leaky 1965, Bishop and Clark 1967, Savage 1978). In comparison, ungulates and predators in modern Holarctic ecosystems appear not to have achieved such equilibrium, probably due to their short history of coexistence spanning only the Holocene (Kurtén and Anderson 1980, Guthrie 1990b, Graham and Lundelius 1984, Martin and Klein 1984). Geist's concept of a more intense predatory regime in North America during the Pleistocene, however, implies that those communities did approach a state of co-evolutionary equilibrium (also see Graham and Lundelius 1984). Under older concepts of the Pleistocene, this seems plausible, but the picture now emerging from paleoclimatic data is that Pleistocene communities probably were not as static as once thought. Instead, it appears that they may have responded to frequent environmental gyrations, ultimately induced by rapidly oscillating climatic conditions. Recent paleoclimatic evidence, particularly from Greenland ice cores, indicates that these fluctuations may have occurred in intervals on the scale of 2000 years, 500 years, and even decades (GRIP 1993, Dansgaard *et al.* 1993, Grootes *et al.* 1993, Field *et al.* 1994, Thouveny *et al.* 1994).

Lister and Sher (1995) recently suggested that these new paleoclimatic data support the notion that climatic variability in the Pleistocene may have been largely responsible for the period's greater biotic diversity by maintaining a more mosaic pattern of habitats. This information, along with our increasing knowledge about fossil diversity, should lead one to question the idea that Pleistocene faunas (or even individual predator-prey relationships) in the Holarctic were able to achieve much significant evolutionary equilibrium, especially during short interglacial periods. Under this emerging picture of the Pleistocene, it seems less likely that Geist's predatory "arms war" would have had enough time to establish the intense co-evolutionary relationships he envisions. Of course, this dilemma alone does not refute Geist's hypothesis. More concrete refutation can be found by re-examining the Pleistocene record of carnivore diversity and body size in North America, Europe, and Asia.

Were there more large predators in North America, and were they bigger than their Old World counterparts? Table 19 lists the species that Geist considered to be part of the large predator fauna in North America (excluding Beringia) during Wisconsinan times. This list of Geist's seems inflated, since a number of the species are not even significantly carnivorous, much less predatory. Species in this category include the Florida cave bear (*Tremarctos floridanus*), the black bear (*Ursus americanus*), and probably the obscure and primitive lesser short-faced bear (*Arctodus pristinus*). More important, the fossil record shows that it is completely unrealistic to think that more than about half of these species were sympatric at any given time (Kurtén and Anderson 1980, Harris 1985, Graham and Lundelius 1995). Lesser short-

TABLE 19. Disparate reconstructions of the large carnivore guilds in North America and Eurasia during the late Pleistocene (Wisconsinan/Würm).

Geist's (1989) list of Rancholabrean carnivores (with comments)	North American species that comprise a realistic and mostly sympatric large carnivore guild, and which potentially threatened humans (* = not on Geist's list)	Carnivore guild of eastern Beringia (it has not been clearly shown that all of these spp. were sympatric or contemporaneous)	Typical representative large carnivore guild of Europe (most spp. shared with Asia)	Total list of Eurasian large carnivores known from the Würm. Compare to Geist's list
Lion (*Panthera leo atrox*)	Lion	Lion	Lion	Lion
Dirk-toothed Sabertooth (*Smilodon spp.*) *Smilodon* and *Homotherium* were seldom sympatric	one sabertooth species	*Homotherium* ?	*Homotherium*?	*Homotherium*?
Scimitar Sabertooth (*Homotherium serum*) *Homotherium* and *Smilodon* were seldom sympatric	Puma	Short-Faced Bear	Leopard	Leopard
Cheetah (*Acinonyx trumani*) distribution unclear, but probably not widespread	Dire Wolf	Brown Bear (Ursus arctos)	Spotted Hyena	Spotted Hyena (*Crocuta crocuta*)
Puma (*Felis concolor*)	Short-Faced Bear	Grey Wolf	Grey Wolf	Striped Hyaena (*Hyaena hyaena*) ?
Jaguar (*Panthera onca*) warm regions only	Grey Wolf (*Canis lupus*) *	Coyote	Dhole	Grey Wolf
Dire Wolf (*Canis dirus*)	Coyote (*Canis latrans*) *	Dhole (*Cuon alpinus*)?	Brown Bear	Dhole (*Cuon alpinus*)
Short-Faced Bear (*Arctodus simus*)	perhaps another medium-sized felid (cheetah or jaguar)		Cave Bear (*Ursus spelaeus*) (not carnivorous but presumed dangerous)	Hunting Dog (*Lycaon lycaonoides*)
Lesser Short-Faced Bear (*Arctodus pristinus*) primitive spp. only known from southern and eastern U.S.; not considered to be a significant predator/carnivore				Brown Bear
Florida "Cave" Bear (*Tremarctos floridanus*) distribution limited to southern North America (mainly southeastern U.S.); probably not significantly carnivorous				Cave Bear (not carnivorous but presumed dangerous)
Black Bear (*Ursus americanus*) not a significant predator or threat to humans				

faced bears, for example, mainly inhabited the eastern seaboard (Kurtén and Anderson 1980, Richards *et al.* 1996), and jaguar only inhabited tropical, subtropical, and mild temperate habitats. They reached up into the northern United States only during warm periods prior to the Wisconsinan Glaciation (Kurtén 1973, Seymour 1993). A generous, but plausible Rancholabrean large carnivore guild might include: short-faced bears, lions, a single sabertooth species (*Smilodon* or *Homotherium*), pumas, perhaps another medium sized felid (cheetah on the plains, jaguar in warm environments), dire wolves, coyotes, and probably grey wolves in the north (Table 19).

Geist does not include *Canis lupus* in his list because the grey wolf is usually considered to be a background or periglacial species south of Beringia until the close of the Pleistocene, when it expanded to become North America's primary Holocene predator. Based on fossil records, grey wolves apparently were seldom sympatric with dire wolves, and it has been suggested that competition between the two mostly kept grey wolves out of central and southern North America (Harington 1977, Kurtén and Anderson 1980). The majority of fossil grey wolves south of the ice sheets are Wisconsinan age, mainly late Wisconsinan, and most are from northern states, but some Illinoisan-age fossils have been found in Nebraska and Arkansas (Nowak 1979, FAUNMAP 1995). In my opinion, there are enough late Pleistocene records of *Canis lupus* in the lower 48 states and southern Canada to consider it to be a significant Rancholabrean predator, at least during the Wisconsinan Glaciation (the wolf's fossil record is discussed more below). The coyote, while not on Geist's list, was a fairly common Rancholabrean canid throughout most of North America, and considering that it was larger than the present form, it also may have been a significant predator of large game (Nowak 1979, Kurtén and Anderson 1980, Harris 1985, FAUNMAP 1995). The coyote's threat to humans, however, may have been minimal, and probably for this reason Geist did not consider it (although this does not seem to be a criterion for his list).

Since the earliest humans entered the New World through Beringia, I will review its specific large carnivore fauna (Table 19). The Wisconsinan large carnivore community of eastern Beringia included the following: lion, grey wolf, short-faced bear, brown bear, probably scimitar cat (*Homotherium serum*), and perhaps the dhole (*Cuon alpinus*) (ecologically, the wolverine played a role in this guild, too, but it does not need to be considered because it is not a threat to humans)(Péwé and Hopkins 1967; Péwé 1975; Guthrie 1968, 1976, 1982, 1990a; Harington 1977, 1978; Matheus 1994b). Because radiocarbon dates on carnivore fossils are quite rare, it is difficult at this point to say how contemporaneous all of these species were, or if they all survived into the late Wisconsinan. For instance, Guthrie (personal communication 1996) suspects that *Homotherium* died out in Beringia before the Wisconsinan, but Harington (1977) reports at least one specimen from near Dawson, Yukon Territory, that appears "very fresh", and he assigns it to the late Wisconsinan. Evidence for the dhole's presence in east Beringia comes from only two fossils, one from Cripple Creek near Fairbanks and the other from Old Crow Locality 14N

in the Yukon Territory (Harington 1977, Kurtén and Anderson 1980). Both specimens are suspected of being Illinoisan age, but the species is known from younger Pleistocene deposits in Northern Asia (but not specifically in northeast Siberia), where it still lives, and a fossil dhole of probable Wisconsinan age has been found in Mexico (Pei 1934, Harington 1977, Kurtén and Anderson 1980). Since it now primarily inhabits woodlands, the dhole most likely was present in Alaska and the Yukon Territory mainly during the last interstadial and interglacial, but, as with other warm-period species, it left few fossils.

Eastern Beringia's large carnivore guild was not terribly divergent from the Rancholabrean guild to the south. Most notably, eastern Beringia lacked 1) *Smilodon* (but *Homotherium* was present), 2) another medium-sized felid (particularly puma), and 3) the dire wolf. (Yesner (1994, 1996) reports a canid humerus from the Broken Mammoth Site in Alaska's Tanana Valley that he believes is from a dire wolf, but its identity is highly questionable because humeri of *C. dirus* are nearly impossible to separate from *C. lupus*.) All carnivores in eastern Beringia, except the brown bear (and probably the dhole), were also found elsewhere in North America. Therefore, eastern Beringia's carnivore fauna appears to be a less diverse, northern version of the Rancholabrean fauna with species particularly adapted for open habitats. (Brown bears migrated to eastern Beringia probably during the early or mid-Wisconsinan, but they did not spread south until about 14,000 B.P., after the Canadian ice-free corridor opened (Kurtén 1960, 1963, 1966a, 1968, 1973, 1976a; Guilday 1968; Kurtén and Anderson 1974, 1980; Harris 1985). Brown bears seem to be the only Siberian large carnivore that immigrated to eastern Beringia during the Wisconsinan.)

The difference between carnivore guilds in eastern Beringia and the rest of North America is not as critical to Geist's hypothesis as is the difference between guilds in eastern and western Beringia—eastern Beringia should have had a more aggressive guild according to predictions of Geist's hypothesis. But the few remains of carnivores found in western Beringia do not differ substantially from those in the east. They consist mostly of wolf and lion, with a few brown bear and a rare *Homotherium* (Sher 1974, 1986, 1987). It is possible that dholes ranged into western Beringia, too. From this perspective, it can be said that eastern Beringia only had one or two "Siberian" carnivores which were lacking in typical Rancholabrean faunas— the brown bear and perhaps the dhole. The only large carnivore in eastern Beringia that did not also inhabit western Beringia was *Arctodus*; Alaska was the northern and western limit of its range (Kurtén and Anderson 1980, Richards *et al.* 1996). Even though it was prevalent in Alaska, *Arctodus* apparently did not cross into Siberia. This is significant in Geist's hypothesis because it points to *Arctodus* as a conspicuous species that could have been excluding humans from eastern Beringia. Considering these patterns, I disagree with Geist's overall vision of the large carnivore guild in Beringia: I would argue that, except for *Arctodus*, the carnivores of eastern and western Beringia were not substantially different, especially in a quantitative sense. However, not much farther west and south of Beringia (i.e., northern China), typical Eurasian elements start to appear, like spotted hyenas (*Crocuta*

crocuta), leopards (*Panthera onca*), and tigers (*Panthera tigris*) (Pei 1934; Colbert and Hooijer 1953; Kurtén 1968; Vereshchagin and Baryshnikov 1982, 1984).

Next, I want to compare these North American carnivores (Rancholabrean and east Beringian) with those in Europe during the last (Würm) glaciation. I think this will show that it is difficult to substantiate Geist's claim of a more intense predatory regime in North America. Europe provides a good comparison because its fossil record is excellent and because predators did not exclude humans from late Pleistocene Europe. European faunas often have high diversities because, in addition to their own indigenous species, they incorporated migrants that originated from Asia and Africa. Table 19 includes a list of known large carnivore fossils from the Würm of Europe (for general reference see Kurtén 1968, 1976b; Vereshchagin and Baryshnikov 1982, 1984; Anderson 1984). A likely large carnivore guild would include: lion, spotted hyena, leopard, grey wolf, brown bear, cave bear (*Ursus spelaeus*) (see qualifications below), and at times *Homotherium*, dhole, hunting dog (*Lycaon lycaonoides*), and striped hyena (*Hyaena hyaena*). As with Geist's list for North America, not all of these species would have been sympatric. Lions, spotted hyenas, wolves, and cave bears are the most common fossil carnivores from late Pleistocene Europe, while others like the hunting dog and *Homotherium* apparently were uncommon (Kurtén 1968). Striped hyenas, too, may have been extinct in Europe before the Würm (Thenius 1980). Renowned European giants like the hunting hyena (*Chasmaporthetes spp.*), the short-faced hyena (*Hyena brevirostris*), and the sabertoothed cat (*Megantereon spp.*) also were extinct in Europe by the end of the late middle Pleistocene (Kurtén 1968, Kurtén and Garevski 1989, Anderson 1984).

There is compelling evidence that the cave bear was primarily an herbivore (Kurtén 1976b, Bocherens *et al.* 1990), but this bear probably was quite dangerous for humans to deal with because it most likely had evolved its huge size, at least in part, as a means to defend itself, implying that it may have behaved aggressively when disturbed (Kurtén 1976b). Indeed, Geist invoked the cave bear in his hypothesis, arguing that it is a good example of a bear that was too dangerous for humans to safely defend themselves against using pre-firearm technology because it was too big. Geist cited the relative lack of archaeological evidence for cave bear hunting in paleolithic sites, and I think this is a sound argument—Holarctic peoples have had diverse bear hunting traditions, but apparently this rarely included cave bears (Kurtén 1976b). However, not all authors agree with this conclusion (Vereshchagin and Baryshnikov 1984).

Carnivore faunas certainly had a different character in Würmian Europe than in North America, but the European fauna does not appear to have been any less diverse, and it would seem difficult to argue that overall predatory pressures were any less intense in Europe. Ungulates and humans in Europe minimally had to deal with various giant felids, huge hyenas, packs of predatory canids of one type or another, big brown bears, plus the cave bear. The existence of Paleolithic archaeological sites indicates

that humans managed to coexist with these species and even successfully hunt most of them.

As further evidence of more intense predation in North America, Geist contended that its predators were larger bodied compared to conspecifics in the Palearctic. I would argue that evidence for this is to the contrary, or at least equivocal. Geist, for example, argued that the North American lion (*Panthera leo atrox*) was the largest-bodied subspecies of Pleistocene lions, and that the largest individuals of this subspecies were found in eastern Beringia. Guthrie (1976) made a similar contention. While it is true that Pleistocene lions were larger than their modern African counterparts, it is contrary to a number of published comparisons of fossils from North America, Europe, and Asia to say that North American lions were significantly larger than those from other regions (Merriam and Stock 1932; Harington 1969, 1977; Vereshchagin 1971; Kurtén 1968, 1985; Kurtén and Anderson 1980). In fact, Kurtén (1985) specifically shows that not only was the European subspecies (*Panthera leo spelaea*) bigger than the North American subspecies (*Panthera leo atrox*), but Beringian lions were smaller than both of those subspecies. (Guthrie (personal communication 1997) disagrees in part with this assessment. He thinks that large European lions are rare, and that the size of lions in Europe is overstated.)

Large lion skulls have been found in eastern Beringia, but this probably is a result of the fact that an unusually large number of fossils have been collected there, providing a better sample of eastern Beringia's overall lion population, including more samples from the extreme ends of the size spectrum. The largest specimens have gained the most notoriety, and in the past collectors had a decided bias for large specimens. Beringia's reputation for large-bodied individuals seems to permeate other species, including *Arctodus*. In fact, it is becoming apparent that many *Arctodus* fossils from areas south of Beringia are in the same size class as the famous large specimens from Alaska and the Yukon Territory (Richards and Turnbull 1995, Richards *et al.* 1996). Beringia's reputation for housing some of the largest-bodied mammals of the Pleistocene is a myth that should be abandoned. The region produces larger individuals today, compared to other regions in the Holarctic, and, while its Pleistocene counterparts were even larger, Beringia's Pleistocene mammals were not any more gigantic than in other regions. In fact, some were smaller. For example, the woolly mammoth (*Mammuthus primigenius*) was the smallest of mammoths, and Beringian horses are dominated by small-bodied forms (Guthrie 1968, 1982, 1990a; Harington and Clulow 1973; Harington 1977; Sher 1974, 1986, 1987; Kurtén and Anderson 1980). Below, I discuss Beringia's diminutive wolf.

Data on fossil jaguars also dispute Geist's notion that late Pleistocene carnivores in North America necessarily evolved larger body sizes. Jaguars evolved in the New World from a larger, archaic species of *Panthera* that migrated from Eurasia during the late Blancan/early Irvingtonian (about 2 million years ago). This ancestor, which probably also gave rise to lions and tigers in the Palearctic, was much larger than modern jaguars, and throughout the Pleistocene jaguars steadily grew smaller (Simpson

1941; Kurtén 1965a, 1973; Kurtén and Anderson 1980, Seymour 1993).

Leopards, hunting dogs, spotted hyenas, dholes, brown bears and wolves of Würmian Europe all were larger than modern conspecifics (see Kurtén 1968, and references cited below for each species). Leopards, hunting dogs, and spotted hyenas did not reach North America, but they were highly successful in Eurasia (Kurtén 1968, 1976b). Compared with modern specimens and with Pleistocene fossils from Africa, these three species were much larger during the Würm in Europe. Yet, it is significant to note that while late Pleistocene leopards in Europe were huge, those in Africa were not much larger than the present form (Kurtén 1968) (following Geist's line of reasoning, this might be taken to mean that predation levels were higher in Europe versus Africa). Hunting dogs are canids adapted for very swift, high-endurance locomotion using highly coordinated group hunting tactics to capture small to medium-sized ungulates in open terrain (Kruuk and Turner 1967, Kruuk 1972, Bertram 1979). They originated in Africa, but apparently inhabited Europe during full glacial times when steppes and periglacial environments dominated (Kurtén 1968). On the other hand, *Cuon* also is a social canid with high endurance, but specializing in large woodland prey (Davidar 1975). Therefore, at any given time in the Pleistocene of Europe, perhaps only one of these canids was present. *Cuon* fossils are by far more common, and have a much longer fossil record in Europe than *Lycaon*, but interglacial and interstadial deposits are better preserved in Europe (Kurtén 1968, 1976b; Anderson 1984). *Crocuta* reached as far north as 56° in Siberia, but it never entered North America (Kurtén 1968, Vereshchagin and Baryshnikov 1984). It may also be relevant that paleolithic humans apparently rarely killed this giant subspecies of spotted hyena, since its modified remains are rare in paleolithic archaeological sites (Vereshchagin and Baryshnikov 1984).

Homotherium inhabited Europe, Asia, and North America, and over much of this range it survived until the end of the Pleistocene. A little smaller than a lion (but built quite differently), *Homotherium* did not differ substantially in size from Texas to Great Britain (Turner (1997) states that late Pliocene to mid Pleistocene *Homotherium* in China were a little smaller than average). Confusion regarding size comparisons in *Homotherium* may be the result of the high degree of sexual dimorphism observed in scimitar-toothed cats and felids in general (Martin and Schultz 1975, Martin *et al.* 1988, Kurtén and Anderson 1980, Kurtén 1985, Kurtén and Werbelin 1990; Marean 1989; Turner 1997).

Brown bears, which seem to have reached eastern Beringia sometime in the Wisconsinan (perhaps earlier), did not colonize areas farther south until the ice sheets receded (about 12,000 to 14,000 B.P.). But again, late Pleistocene brown bears both in Beringia and Europe were huge (Kurtén 1958, 1960, 1965b, 1968, 1976b; Kurtén and Anderson 1980). Geist's hypothesis specifically predicts that species like the brown bear should have become larger as it entered eastern Beringia, in response to intense competition and predation. This does not appear to be the case in brown bears

Wolves do not conform to Geist's predictions, either. The European wolf of the last interglacial (Eem) and glacial (Würm) were somewhat larger than present (Kurtén 1965b, 1968). Wisconsinan-age wolf fossils from North America south of Beringia present an unclear picture, as very large and very small specimens have been found there, sometimes at the same sites. However, it is not clear whether these two morphs were contemporaneous (Nowak 1979). There also is a notion that Pleistocene wolves in eastern Beringia were smaller than present (Guthrie personal communication 1995), but this idea has not been tested well. Based on limited available data, Harington (1977) suggested that late Illinoisan and Sangamonian wolves in the Yukon Territory may have been smaller than present, but he did not draw conclusions about Wisconsinan wolves. Table 26 in Harington (1977) lists mandibular dimensions for two wolves of probable Wisconsinan age, but that is too few to make a firm conclusion.

To address this issue of Pleistocene wolf size, I measured condylobasal lengths on fossil wolf skulls (n = 22) of presumed Wisconsinan-age from the Fairbanks area and compared them to 38 modern skulls (20 males and 18 females) from the same region (Tables 20 and 21 and Fig. 26). The size distribution and statistics seem to verify that east Beringian wolves were smaller than present, but only by about 4% (one-tailed two sample t-test, assuming unequal variances: t Critical = 2.0223, T = 3.5127, df = 39; p ($T \leq t$) = 0.00057).

Sampling biases, however, probably overestimate the difference between modern and fossil wolves. For instance, I made my measurements on modern wolves in the University of Alaska Museum that were collected mostly from fur-trappers. Typically, trappers configure their equipment and operation to capture the largest wolves possible. Furthermore, for both modern and fossil wolves, I excluded specimens that exhibited juvenile traits, such as clearly open cranial sutures or teeth that were not fully erupted. Even with this precaution, it is easier to exclude juveniles from a collection of modern, complete skulls than from incomplete and damaged fossil skulls.

The distribution of the data in Fig. 26 indicates that sampling bias for smaller (younger?) individuals was greatest among modern males, based on the data's leftward skew (skewness, g_1 = -0.62337), whereas the skewness in modern females is slight and to the right (g_1 = +0.13531). However, neither males nor females show much variation in skull length (S.D. = 7.1 and 7.2, respectively) compared to Pleistocene wolves (S.D. = 10.3). I conclude that the Pleistocene distribution represents a fairly good sampling of the whole population and contains roughly equal numbers of males and females because the sample's standard deviation is similar to the combined standard deviation of modern males and females (S.D. = 9.5). The slight leftward skew of the Pleistocene distribution (g_1 = -0.3339) suggests that somewhat more young individuals were being preserved as fossils. Today, young, dispersing wolves have a higher mortality rate than non-dispersing adults (Wasser 1996); this pattern also may explain the skew towards smaller individuals in the fossil wolves. Juvenile male and juvenile female wolves disperse

from natal territories with equal frequency in modern populations, and both experience high mortality during dispersal (Waser 1996), so the size distribution of Pleistocene wolves cannot be used to indicate any discernable difference in mortality among males and females.

Kurtén (1968) published a diagram (but no data values) showing that European wolves were a few percent larger than present during the last glacial and interglacial. My data show that east Beringian wolves from the Wisconsinan were smaller by a few percent. Even though body sizes of modern and Pleistocene wolves in the two regions are significantly different (see statistics above), the differences are small, and considering potential taphonomic and sampling biases, it probably is best to conclude that late Pleistocene wolves were *about* the same size as present, both in Europe and eastern Beringia. This is an interesting pattern because it differs from that seen in most other Pleistocene large mammals.

I can offer two preliminary ideas which may explain this pattern. First, *C. lupus* has been slowing evolving a larger body size ever since its divergence from *C. etruscus* in the Villafranchian/Irvingtonian (Pei 1934, Kurtén 1968), and unlike most other large mammals, it did not experience post-Pleistocene dwarfing. Since there was no late Pleistocene gigantism in wolves, they did not have a "pre-gigantic" size to which they returned in the Holocene, and we may be simply observing a continuation of its slow trend to larger size. Second, with a higher diversity of carnivores and more intense competition in the Pleistocene (throughout the Holarctic, not just North America), principles of resource partitioning and competitive exclusion predict that if some carnivores became larger, others would become smaller, in order to subsist on smaller prey. This also may explain why Pleistocene jaguars show a trend towards smaller size (i.e., they made a niche out of hunting smaller prey). In a sense, the wolf became relatively smaller compared to other carnivores in the Wisconsinan/Würm by not getting larger, because other carnivores did increase body size. What may be occurring in Holocene wolves is an increase in body size due to competitive release following the extinction of other, larger carnivores. In terms of Geist's hypothesis, the wolf data dispute his prediction that this prevalent carnivore was larger in Beringia, compared to Eurasia, and I have not seen data demonstrating that they were universally larger in the rest of North America either (Nowak's 1979 data is equivocal).

Comparisons between the large carnivores of North America and Asia reveal similar patterns to those seen between North America and Europe— and in Asia there is the added consideration that additional giant predators were present, such as the tiger (in woodlands), which ranged far into the north and grew to a huge size in the Pleistocene (Pei 1934, Colbert and Hooijer 1953). Giant Lions, hunting dogs, cheetahs, wolves, brown bears, and tigers placed Asia's large carnivore community on par with those in North America and eastern Beringia. Viewing the situation from the standpoint of carnivore diversity and size, it seems exceedingly difficult to argue that overall predatory pressures were escalated

TABLE 20. Skull measurements of modern wolves collected from central Alaska, mostly near Fairbanks.

specimen	collection locality	sex	condylobasal length	zygomatic width
UAM 28899	Fairbanks	m	237	145
UAM 17341	Fairbanks	m	240	140
UAM 17265	Fairbanks	m	241	150
UAM 17090	Fairbanks	m	245	144
UAM 17154	Fairbanks	m	248	146
UAM 17348	Fairbanks	m	249	149
UAM 28906	Healy	m	249	144
UAM 2188	Big Delta	m	252	147
UAM 17349	Fairbanks	m	253	145
UAM 18391	Fairbanks	m	253	149
UAM 17261	Fairbanks	m	254	148
UAM 18249	Fairbanks	m	255	150
UAM 17345	Fairbanks	m	255	157
UAM 17242	Fairbanks	m	256	150
UAM 17351	Fairbanks	m	256	146
UAM 17353	Fairbanks	m	257	154
UAM 3416	Tanacross	m	258	156
UAM 28909	Fairbanks	m	259	148
UAM 31718	Minchumina	m	261	160
UAM 28907	Healy	m	264	160
UAM 28898	Fairbanks	f	228	133
UAM 2187	Big Delta	f	230	123
UAM 28904	Fairbanks	f	232	133
UAM 28908	Fairbanks	f	233	140
UAM 17257	Fairbanks	f	234	136
UAM 28910	Fairbanks	f	235	132
UAM 17356	Fairbanks	f	236	140
UAM 28901	Fairbanks	f	237	128
UAM 17174	Fairbanks	f	238	137
UAM 28902	Fairbanks	f	239	137
UAM 17318	Fairbanks	f	242	146
UAM 17369	Fairbanks	f	242	138
UAM 28903	Fairbanks	f	243	140
UAM 28900	Fairbanks	f	247	141
UAM 28905	Healy	f	249	142
UAM 18045	Fairbanks	f	249	147
UAM 17317	Fairbanks	f	249	142
UAM 28911	Fairbanks	f	251	146

Table 21. Skull measurements of fossil wolves collected from central Alaska. All except one from Manley Hot Springs and one from Wiseman come from the immediate vicinity of Fairbanks.

specimen	collection locality	condylobasal length	zygomatic width
AMNH 30433	Fairbanks vicinity	214	126
AMNH 30458	Goldstream	215	118
AMNH 30457	Cleary Creek	223	132
AMNH 67157	lower Goldstream at Fox	225	131
AMNH 67158	Engineer Creek, Dawson cut	230	138
AMNH 67164	lower Goldstream at Fox	230	130
AMNH 30432	Fairbanks vicinity	232	135
AMNH 67159	Cripple Creek	234	140
AMNH 67167	lower Goldstream	234	148
AMNH 67160	Little El Dorado Creek	236	142
AMNH 67166	upper Cleary Creek	236	142
AMNH 30452	Manley Hot Springs	238	140
AMNH 67163	Ester Creek	238	146
AMNH 30431	Fairbanks vicinity	241	140
AMNH 67170	Ester Creek	241	152
AMNH 67165	Gilmore deadline	242	146
AMNH 30451	gravel drift at upper Cleary	244	144
AMNH 30450	lower Goldstream	244	154
AMNH 30453	Goldstream	246	145
AMNH 67169	Fairbanks Creek	247	145
AMNH 97079	Wiseman	255	152
AMNH 30430	Goldstream	256	--

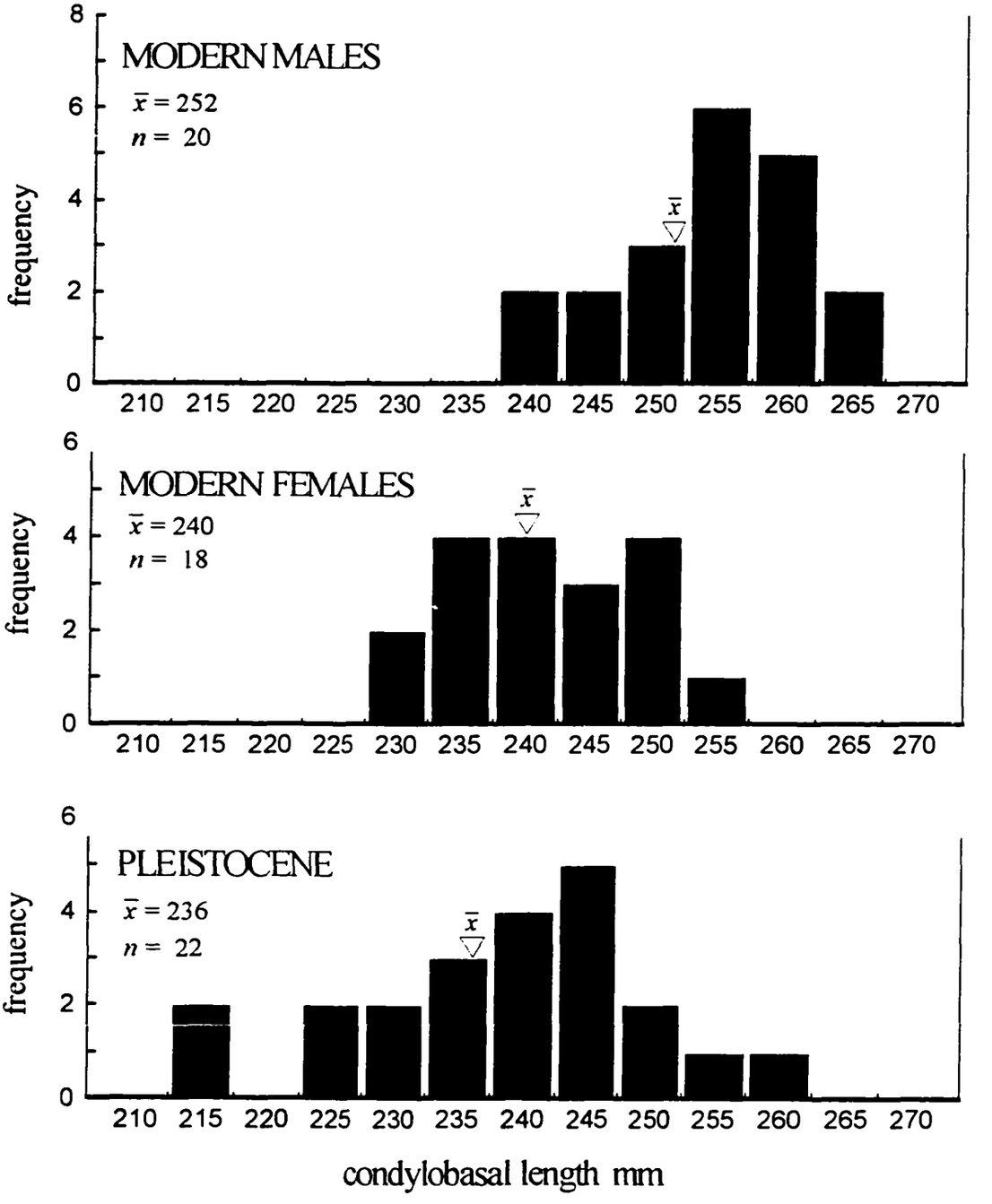

FIGURE 26. Skull sizes in late Pleistocene and modern wolves (*Canis lupus*) from interior Alaska. Interior wolves were actually smaller bodied during the Wisconsinan, unlike most large mammals, but it is not known whether this reflects an ecophenotypic size change within a continuous population, as opposed to a Holocene replacement by a larger-bodied population. All samples were collected within 200 km of Fairbanks.

in North America. Nearly all of the carnivores mentioned were huge throughout their range in the Pleistocene, not just in North America. And while it may even be true that their large size was in response to larger bodied prey, it would seem that this phenomenon was not unique to North America. However, there was one major way that the carnivore community of the Old World differed from that in North America— Europe and Asia did not have a super-huge bear.

NEW DATA ON SHORT-FACED BEARS

New Ecological and Behavioral Data

The giant short-faced bear truly has been an enigma to paleontologists. Its size and highly derived morphology (large size, large, robust skull, and long, gracile limbs— Fig. 25) have led to a broad range of suggestions regarding its probable diet, behavior, and overall ecology. *Arctodus'* morphology and size at first puzzled researchers, and early anatomical descriptions were tied to questions of taxonomy and geographic variation (Cope 1879, 1891; Lambe 1911; Barbour 1916; Merriam 1911; Merriam and Stock 1925). Since its discovery and identification, *Arctodus* has been compared to felids because there are some superficial anatomical resemblances and convergent features (Barbour 1916, Kurtén 1967). This comparison led to the assumption that there were commensurate ecological and dietary similarities to large felids— planting the notion that short-faced bears were predatory. Kurtén (1967) published the first thorough overview and interpretation of *Arctodus'* morphology and distribution; the paper culminated in Kurtén's suggestion that *Arctodus* was a swift predator specialized for hunting Pleistocene megaherbivores. Kurtén's model of *Arctodus'* ecology, re-iterated in Kurtén and Anderson (1980), became the widely accepted paradigm for this species, and his 1967 paper is still regarded as the most authoritative work on *Arctodus*. His reputation as an expert on fossil bears and the large scope of Kurtén's 1967 publication has made it difficult to challenge his model.

Emslie and Czaplewski (1985) tried to refute Kurtén's predatory model by pointing out some weaknesses in his morphological assessments and ecological conclusions. They especially challenged the notion that *Arctodus'* limbs were cursorily-adapted, and they argued that its dentition lacked the sectorial modifications expected in a carnivorous bear. They also chose to emphasize similarities between *Arctodus* and its closest living relative, the extant spectacled bear (*Tremarctos ornatus*) of South America, which is almost exclusively herbivorous. Citing body size patterns in Eisenberg (1980), these authors further suggested that *Arctodus* was well beyond the size range of any known terrestrial carnivore, necessarily relegating it to a life of herbivory (based on energetic constraints). The shortcoming of Emslie and Czaplewski's work is that it falls short of a cohesive analysis. Pointing to possible flaws in Kurtén's work does not necessarily support their alternative model, and the rationale they use to conclude that *Arctodus*

was predominately herbivorous does not have a very firm foundation.

Emslie and Czaplewski's herbivore model has received little acceptance among paleontologists, and over the past 30 years, most authors who mention *Arctodus* invariably make reference to its assumed role as a carnivore, and specifically a predator (e.g., Harington 1973, 1977, 1991; Voorhies and Corner 1982; Nelson and Madsen 1983; Agenbroad 1990; Agenbroad and Mead 1986; Guthrie 1988, 1990a, Richards and Turnbull 1995; Richards *et al.* 1996). Geist followed this tradition by expounding on its implications to humans and ungulates. However, up to now, little conclusive evidence has been put forth to justify these specific inferences regarding *Arctodus*' ecology, behavior, and role in Pleistocene ecosystems. Without such firm evidence, any suggestion as to *Arctodus*' influence on human expansion is quite speculative.

Recently I presented such evidence and proposed a new model of *Arctodus*' niche (Matheus 1994a, 1995). First, using carbon and nitrogen stable isotope ratios in collagen extracted from *Arctodus* fossils, I established that *Arctodus* was highly carnivorous (Fig. 27). Figure 27a shows the range of isotopic signatures predicted for carnivores and herbivores (compiled from isotope ratios in modern terrestrial consumers), Fig. 27b shows the actual isotope values in the bone collagen of 24 modern brown bears from interior Alaska, and Figure 27c depicts the values recovered from purified bone collagen of 16 short-faced bear fossils from Alaska and the Yukon Territory. The high $\delta^{15}N$ values found in *Arctodus* reveal that it clearly was carnivorous. The tight cluster of data also indicates there was not a large amount of variation in diets (trophically) between individual bears. It may be significant, however, that increasing $\delta^{15}N$ values are commensurate with a trend towards decreasing $\delta^{13}C$ values. In some cases, researchers studying modern consumers have noted a tendency for $\delta^{13}C$ to become slightly *enriched* by trophic steps (up to about 1 part per mil per step), but a trophic *depletion* of ^{13}C is not known (DeNiro and Epstein 1978, Chisholm *et al.* 1982, Schoeninger and DeNiro 1984). If there was significant trophic variation within the sampled bears, then rising $\delta^{15}N$ values should be accompanied by decreasing $\delta^{13}C$ values. Since this does not occur, it suggests that rising $\delta^{15}N$ values in *Arctodus* do not reflect increasing trophic position, but instead indicate that the meat being consumed came from more than one source. Alternatively, the variation in $\delta^{13}C$ may reflect climatic variation over time (due to slight changes in the physiology and/or type of primary producers). Testing this hypothesis would require radiocarbon dating all the samples to see if $\delta^{13}C$ values (or $\delta^{15}N$) vary in concordance with known climatic intervals.

I also have reconsidered the functional and ecological significance of *Arctodus*' specialized morphology (Matheus 1995, also see Chapters 1 - 3). Its locomotor features, while decidedly cursorial, appear to be adapted *not* for generating high top speed, nor for acceleration, but rather for highly efficient, sustained locomotion— i.e., endurance. Since most predators rely on either high top speed (pursuit) or

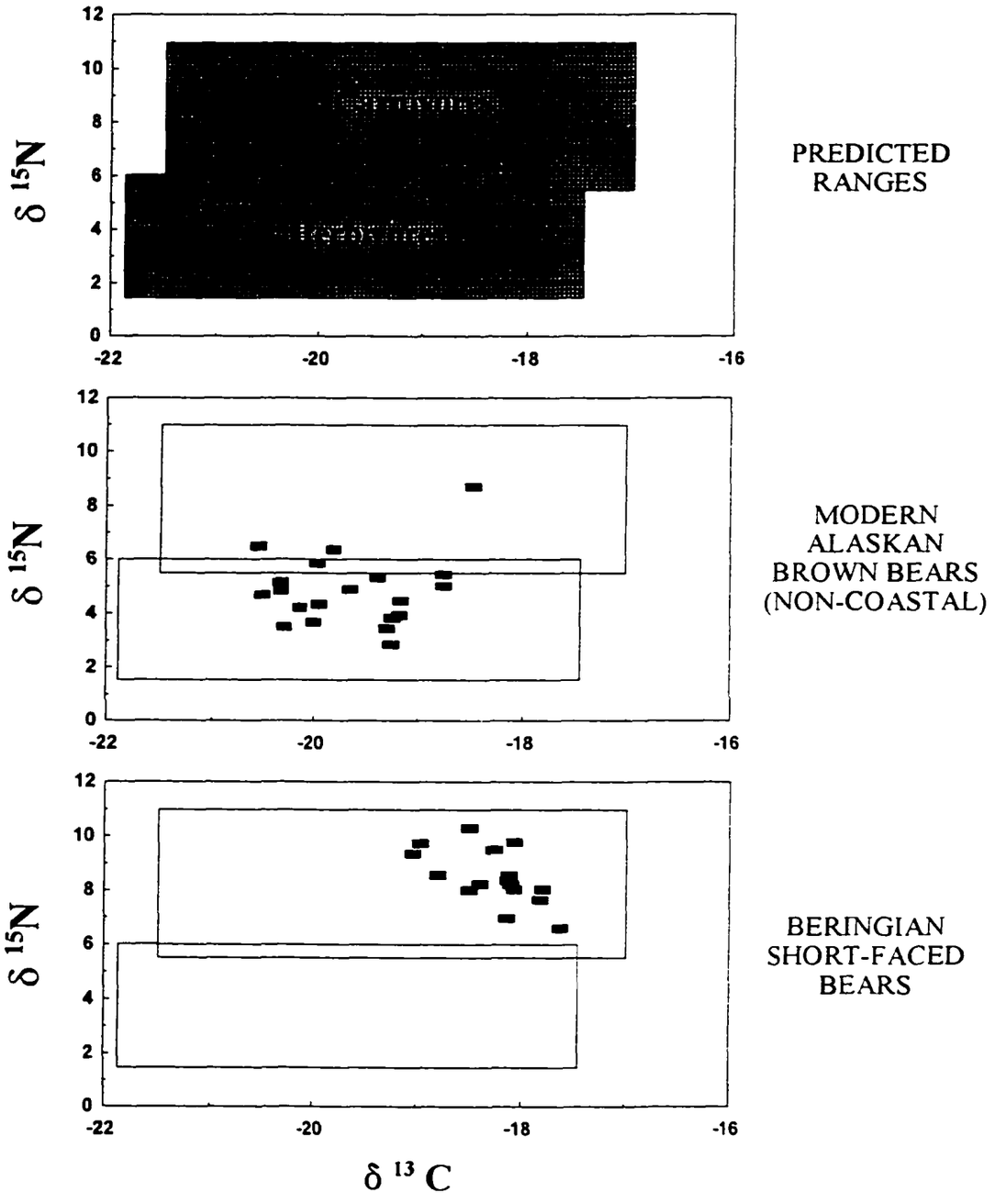

FIGURE 27. Stable carbon and nitrogen isotope values in Beringian short-faced bears (lower graph), compared to values in known carnivores and herbivores (upper graph) and data from modern brown bears of interior Alaska (middle graph). The modern brown bear data demonstrate how stable isotopes accurately reflect this species' omnivorous, but mostly vegetarian, diet. In comparison, the data for short-faced bears reveals that it was highly carnivorous. Isotopes were measured in purified bone collagen extracted from well-preserved fossils.

rapid acceleration (ambush) to capture prey, and since *Arctodus* seems to have had neither, I proposed that *Arctodus*' most likely functioned as a specialized scavenger that was built to cover a large home range in order to seek out widely dispersed carrion (some predators, particularly large canids, use long range pursuit, and they, too, are built for endurance. However, this seems an unlikely strategy for *Arctodus* since most pursuit predators are much smaller and almost always hunt socially).

Other features of *Arctodus* also are more consistent with a scavenging role. Its light build functioned to increase locomotor efficiency, but this meant sacrificing some strength. However, its huge size meant that its *absolute* strength was far greater than any other carnivore on the landscape. Its seems, therefore, that its combined large size and slender build were adaptations to increase locomotor efficiency while still allowing *Arctodus* to dominate other carnivores. In an ecosystem with a low biomass of large mammalian prey and few available carcasses, there would be great incentive for a scavenging specialist to evolve such a competitive dominance. Thus, an important part of the scavenging hypothesis is that *Arctodus* was large and aggressive in order to procure and defend carcasses from other large carnivores (Matheus 1995, also see Chapters 3 and 4).

As one example of a specific morphological feature that may reflect this aggressive behavior, consider *Arctodus*' pelvis. The neck of the ilium is considerably wider and thicker than in other bears, a trait which has perplexed paleontologists (Richards and Turnbull 1995). By modeling some mechanical features of *Arctodus*' spine, hip, and femoral abductors it becomes apparent that the thickened neck of the ilium would be highly advantageous for a bear that frequently stood upright (Fig. 24, Chapter 3). A bipedal stance may have been used for intimidation since it would have had the effect of increasing a bear's apparent size, and allowing a bear to use its front limbs as weapons.

The scavenging model also is consistent with *Arctodus*' cranial morphology, which indicates a very strong masticatory apparatus and a mechanical configuration that imparted strong occlusal forces to the distal teeth, especially during a half-gape. Considering the high amount of wear present on the P^4 of adult *Arctodus* fossils, I argued it was probable that short-faced bears used this tooth as a bone cracking hammer, in conjunction with the talonid of M_1 (Matheus 1995, also see Chapter 4). To some, it may seem heretical to suggest that the carnassials were used in this manner, but *Arctodus* inherited typical unspecialized, ursid carnassials, and in my opinion, these did not form a functional shear surface, and thus were of limited use for cutting flesh. On the other hand, their distal position and conical shape made *Arctodus*' carnassials excellently pre-adapted for use in cracking cortical bone because *Arctodus*' shortened rostrum brings the distal teeth closer to the jaw articulation (fulcrum), increasing the mechanical advantage to these teeth and thereby imparting more force to them. The conical shape of P4 and the trigonid of M1 mean that bite forces were concentrated at their apices, which is a configuration necessary for initiating the cracking process in a dense, composite material like cortical bone. Bone-

cracking is a recurrent theme among scavengers, since opening up bones enables them to extract the maximum nutritional content of a carcass (i.e., accessing lipids in marrow and eating whole bone). This is an important asset for scavengers since any carcass they find may already be cleaned of flesh by other carnivores. The wide pallet and gullet of these bears indicate that they also may have swallowed relatively large, minimally processed pieces of flesh and bone, which might imply that *Arctodus* had a specialized gut and could digest bone, like spotted hyenas (Ewer 1967, Sutcliffe 1970, Kruuk 1972).

I think it is informative to consider how *Arctodus'* dentition differs so much from the only other bear which has evolved towards exclusive carnivory— the polar bear (*Ursus maritimus*). Polar bear cheek teeth are unique among bears. In their brief evolution (probably < 700,000 years), polar bear teeth have evolved rapidly towards increased slicing duties to match their carnivorous niche (Kurtén 1964). Polar bear teeth are more trenchant and reduced in size, particularly in their width, compared to all other ursids, forming a molar battery of taller, narrower teeth with increased sectorial capabilities. *Arctodus*, which was carnivorous according to isotope data, had a slightly longer evolutionary history (about one million years) (Kurtén 1967), yet it shows opposite tendencies to polar bears; *Arctodus* retained broad, robust molars and it had evolved little sectorial ability. For a carnivorous animal, this can have little advantage unless the animal is processing very durable material in the diet— most likely bone in this case.

It seems that whereas the predator and herbivore models for *Arctodus* have inconsistencies, the scavenger model most congruously links all the data for this unusual bear— from stable isotopes to cranial features to total post-cranial design. Information from stable isotopes eliminates the herbivore model, and, morphologically, it is difficult to demonstrate how *Arctodus* was specifically adapted to be a predator, since it could not catch particularly fast prey, nor did it have the acceleration necessary to be an ambush predator. And, if *Arctodus* preyed on large, slow pachyderms, it seems unlikely that selection would favor such a gracile build.

Implications of Arctodus' Scavenging to Human Occupation

In this chapter, my goal is not to recapitulate all the argument contending that *Arctodus'* was a scavenger, but rather to point out the model's implications for humans. If *Arctodus* was a predator (Kurtén's and Geist's models), this would have meant that a large, lethal carnivore was prowling the landscape, perhaps posing a direct threat to humans, who were apparently too poorly armed to defend themselves against a large, predatory bear. However, it is difficult to demonstrate that a predatory bear, even the size of *Arctodus*, would have had such an aggressive disposition as to absolutely exclude humans. This seems to be the key element missing in Geist's hypothesis. But in fairness to Geist, that is why he developed the argument that North America's large carnivores were so highly competitive and aggressive's and too dangerous for humans.

Earlier, I pointed out that the evidence for Geist's carnivore scenario is lacking; it seems difficult to argue that North America, and Beringia in particular, had a more intense predatory regime than Europe and Asia (where humans managed to persist). However, the scavenging model specifically predicts that *Arctodus* was aggressive, sought out meat resources, and keyed in on the activities of other predators, potentially including humans. Therefore, the implications to humans are much less speculative: humans themselves and their meat resources (kills and caches) would have been under constant threat by short-faced bears in eastern Beringia. So, despite my refutation of Geist's main argument, perhaps the presence of *Arctodus* in North America still remains the single key feature distinguishing Nearctic and Palearctic carnivore faunas in the late Pleistocene.

New Radiocarbon Dates

Geist's thesis rests critically on two temporal considerations: 1) the timing of the earliest human occupation of far Northeast Asia, and 2) the time period that *Arctodus* inhabited Alaska— in particular, the timing of its extinction there.

There is no strong archaeological evidence for human occupation of far northeast Siberia (especially the Chuckchi Peninsula) prior to about 14,000 to 18,000 B.P., depending on author (Dikov 1978; Yi and Clark 1985; Clark 1988; Grayson 1988; Powers 1990, 1996; Kelly 1996), even though sites appear elsewhere in Siberia perhaps as early as 35,000 B.P. (Mochanov 1978, Müller-Beck 1982). But even these are most likely less than 20,000 B.P. (Yi and Clark 1985, Clark 1988). Guthrie (1996) and others (e.g., Powers 1990 and Haynes 1982), doubt that humans were poised on the edge of Alaska much before 12,000 B.P.. Guthrie (1996) expounded the notion that the ancestors of the first Americans (neomongoloids) were biologically and technologically adapted to the mammoth steppe environment and he contended that neomongoloids diverged from a paleomongoloid stock during the last interstadial and expanded north, but did not reach Alaska during that early expansion. Their range contracted southward during the glacial maximum and expanded again in conjunction with woody environments during the subsequent Birch Period (ca. 14,000 B.P.), finally culminating in their habitation of the New World shortly thereafter. In contrast, Geist did not totally reject the notion of much earlier human occupation in eastern Beringia, which is based on controversial evidence from the Yukon Territory's Old Crow Basin. In fact, he used it as an indication that neomongoloids (Guthrie's term) made forays into North America during their interstadial expansion, but failed to gain permanent footing until the last few millennia of the Pleistocene. Geist said the reason for this failure primarily was the presence of *Arctodus*, among other large, aggressive carnivores.

Geist's scenario presumes that short-faced bears were in eastern Beringia throughout the late Pleistocene and it predicts their extinction should slightly precede the earliest unequivocal date of

permanent human occupation. This date currently stands around 11,500 to 12,000 B.P. (Powers, 1990, Hoffecker *et al.* 1993), a date Geist agrees with. This, in fact, is the terminal date for *Arctodus* in the rest of North America (Kurtén and Anderson 1980, Nelson and Madsen 1983, Gillette and Madsen 1992), and Geist assumes that this date is valid for Beringia, too. Based on their position in Pleistocene muck deposits, most *Arctodus* fossils in Beringia most likely date to the Wisconsinan period, while a few are probably Illinoisan or maybe older. But up to now, only three radiocarbon dates have been published on Beringian *Arctodus*. Table 22 lists these three dates and 8 new dates— five from this study, and 3 unpublished dates communicated by C.R. Harington. Figure 28 depicts the 11 dates graphically. These data, while limited, suggest that *Arctodus* was present in eastern Beringia during the interstadial as well as early stages of the glacial maximum, but there are no dates younger than about 20,000 B.P. (uncalibrated). One must be cautious about making conclusions based on a lack of dates from a certain period, and eleven dates are by no means exhaustive. But even with these considerations, the radiocarbon data suggest that *Arctodus* did not survive the glacial maximum in Beringia.

There are a number of important paleoecological implications to be drawn from this conclusion, but, in terms of this discussion, it suggests that *Arctodus* was extinct in Alaska before humans were poised to cross the Bering Land Bridge. Geist's notion that *Arctodus* may have put an end to interstadial forays of humans into the New World also is not supported by the radiocarbon data— otherwise one would expect the earliest permanent archaeological sites in Alaska to be just under 20,000 B.P. That is to say, if *Arctodus* was precluding early human attempts to permanently inhabit eastern Beringia, then as soon as *Arctodus* became extinct (≈ 20,000 B.P.) humans should have appeared. I am not vehement about this point, however, because it would assume that Paleolithic Asians had the capability to survive in the Arctic during the peak of the last glacial maximum. Indeed, the lack of full-glacial archaeological sites from northern Europe and Asia indicates that extreme northern environments were uninhabitable by humans, given their level of technology at that time (Soffer and Gamble 1990).

Any future discovery of Beringian *Arctodus* fossils substantially younger than 20,000 B.P., or the discovery of considerably older archeological sites in eastern Beringia, will nullify most of the above reasoning. Older archaeological sites have been sought for quite some time, but continue to seem less likely. However, it would not be so surprising for a younger date on *Arctodus* to turn up. At this point, it seems that the timing of key events does not support Geist's hypothesis.

These conclusions would suggest that no human ever laid eyes on a short-faced bear— however, that may not be the case. An *Arctodus* specimen, dated to 12,650 ± 350 B.P., from the Lubbock Lake site in Texas, is reported to show signs of butchering (Johnson 1987). If this report holds up to scrutiny, then paleoindians south of Beringia apparently encountered this giant bear— and survived. To some, this evidence alone may disprove Geist's hypothesis.

TABLE 22. Uncalibrated radiocarbon dates for short-faced bears in Beringia (normalized to $\delta^{13}C$ = -25 ‰). AMS dates on collagen, conventional dates on whole bone. Error is ± 1 standard deviation.

Specimen	Locality	^{14}C Age	Lab No.	Method [1]	Source [2,3]
YG 24.1	Ophir Creek, Dawson loc. 77	20,210 ± 110	Beta-79852	AMS	a
(=CRH 95-3)			CAMS-18415	AMS	a
F:AM 30492	Cleary, Fairbanks Area, Alaska	20,524 ± 180	AA-17511	AMS	this study
NMC 50367	Hunker Cr., Dawson Loc. 37, Yukon	24,850 ± 150	TO-3707	AMS	a
F:AM 30494	Ester, Fairbanks area, Alaska	25,496 ± 224	AA-17512	AMS	this study
NMC 7438	Gold Run Cr., Dawson area, Yukon	26,040 ± 270	TO-2996	AMS	a, b
ROM:VP 43646	Ikpikpuk River, north slope, Alaska	27,190 ± 280	TO-2539	CONV	c
A-37-10	Upper Cleary Cr., Fairbanks area, Alaska	27,511 ± 279	AA-17513	AMS	this study
NMC 37577	Lower Hunker Cr., Dawson Loc. 10, Yukon	29,600 ± 1200	I-11037	CONV	a, b
"Birch"	Birch Cr., 180 km northeast of Fairbanks	34,974 ± 652	AA-17515	AMS	this study
AMNH 99209	Ester, Fairbanks area, Alaska	39,565 ± 1126	AA-17514	AMS	this study
NMC 42388	Sixty mile Loc. 3, Yukon	44,240 ± 930	TO-2699	AMS	a

[1] **AMS** = accelerator mass spectroscopy dating; **CONV** = conventional dating

[2] ***Sources*** a - C.R. Harington, personal communication; b - Harington 1989; c - Churcher *et al.* 1993. d - John Cook, personal communication

[3] dates from this study are AMS dates on collagen purified with chromatography resins— see discussion in Methods section of Chapter 1

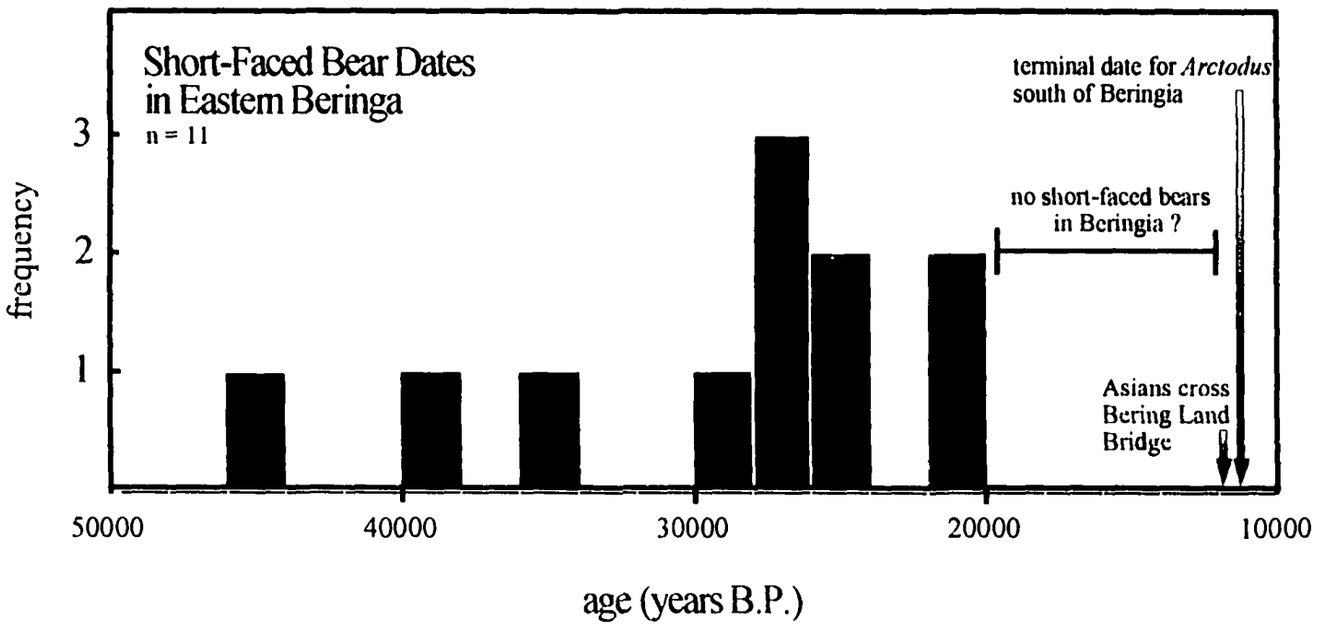

FIGURE 28. Distribution of all known radiocarbon dates for Beringian short-faced bears (data from Table 1). *Arctodus* was present in eastern Beringia through the last interstade and the beginning of the last glacial maximum, but the data tentatively suggest that *Arctodus* died out in Beringia shortly after 20,000 B.P.. The gap of nearly 8000 years between *Arctodus*' apparent extinction and the oldest verifiable archaeological sites in eastern Beringia (= 11,800 B.P.) is inconsistent with Geist's contention that short-faced bears were excluding humans from North America.

SUMMARY

Val Geist (1989, 1994) presented a biologically insightful and creative hypothesis— that short-faced bears and other North American carnivores were too large and aggressive for Pleistocene humans to defend themselves against, and thus they presented the main obstacle to Asians trying to inhabit the New World at the end of the Pleistocene. Geist's hypothesis centered on two key arguments, which I have disputed: 1) Geist argued that, compared to Pleistocene Eurasia, North America's Rancholabrean fauna was characterized by more intense predation imparted by more aggressive predators, and 2) Geist contended that North America had a unique and very large predator in the short-faced bear— a predator which humans were not equipped to defend themselves against. The premises of Geist's hypothesis are biologically and anthropologically sound, but the hypothesis has several flawed assumptions, and it is difficult to reconcile it with the fossil record of large carnivores.

First, body size data do not support Geist's argument that North American predators were larger than in Europe and Asia; throughout the Holarctic, Pleistocene carnivores displayed nearly equal levels of gigantism (and probably aggression). Second, I refuted the assumption that *Arctodus* was an active predator. Recent stable isotope data and mechanical analyses of *Arctodus*' morphology more consistently support the alternative hypothesis that *Arctodus* was a specialized scavenger. The scavenging hypothesis specifically predicts that short-faced bears were aggressive and skilled in locating and procuring meat resources from other predators, which would have included humans. Theoretically, this would have made *Arctodus* even more of a threat than if it was strictly predatory. Thus, Geist's hypothesis is compelling because the presence of *Arctodus* in North America indeed may have been the most critical factor distinguishing carnivore guilds in Palearctic and Nearctic during the Pleistocene.

Geist's hypothesis still should be tentatively rejected, however, because current data on the chronology of short-faced bears in Beringia and humans in northeast Siberia and Alaska are inconsistent with Geist's predictions about the timing of human migration events. It appears that humans probably were not poised to enter Alaska until about 12,000 to 14,000 years ago, and all eleven known radiocarbon dates on *Arctodus* indicate that it may have become extinct in Beringia shortly after 20,000 B.P. When Geist presented his hypothesis, these facts were not readily apparent.

Geist's hypothesis essentially has been ignored by anthropologists. Perhaps this is because it seems so incredible, but also because at first it may appear impossible to test or refute. I have tried to show that this is not the case, as the hypothesis has specific predictions and assumptions which can be tested. It seems important to use this exercise not only to remind ourselves that difficult questions like these can be tested in the paleo-record, but that the biological and evolutionary limitations of humans should not be ignored. Indeed, if new dates on humans or short-faced bears in Beringia fill the chronological gap

between the two, then anthropologists will have to seriously re-ask Geist's question of whether "humankind's single most ferocious predator" foiled early attempts by Asians to inhabit North America.

ACKNOWLEDGMENTS

I would like to thank Val Geist for providing such a provocative hypothesis to test, and one which compelled me to present this paper at the 1996 Alaska Anthropological Association Meeting. While I disagree with his conclusions regarding *Arctodus*, I respect Val Geist as a leading theoretician in mammalian evolutionary ecology. Likewise, many thanks are extended to Dale Guthrie, whom I was fortunate enough to study under at UAF. Any abilities I may have to read and interpret the fossil record or understand mammalian ecology are owed to him. C.R. Harington continues to provide critical data and ideas regarding Pleistocene chronologies in Beringia, and I thank him for generously allowing me to present three of his unpublished radiocarbon dates. Any reference to those three dates should credit him. We are fortunate to have creative practitioners like Geist, Guthrie, and Harington who not only formulate innovative hypotheses, but also test them with the grit of real-life experiences. I thank the NSF-University of Arizona AMS lab for providing five other radiocarbon dates, and especially Rosemary Maddock for her kind assistance there. Thanks to Craig Gerlach and David Yesner for a superb job organizing this session on zooarchaeology— thanks especially to Craig for remaining upright and in his chair during my presentation. Finally, a big thanks to Toos, for her help with this manuscript and especially for all her patience.

APPENDIX 1

STABLE ISOTOPE VALUES (CARBON AND NITROGEN) OF CARNIVORA FROM PLEISTOCENE BERINGIA AND MODERN AFRICA

In any study such as this, where stable isotope levels in animal tissues are used to infer information about paleodiets, it is necessary to state the basis for interpreting isotope results. Figure 1 in Chapter 1, for instance, displays the range of isotopic signatures (collagen values) predicted for bears based on three dietary categories— C_3 herbivory, terrestrial C_3 carnivory (consuming C_3 herbivores), and marine carnivory (salmon feeding). The predicted isotopic ranges for these categories were constructed based on published data sets generated from modern consumers in northern Holarctic ecosystems and from similar categories erected by other authors (e.g., DeNiro and Epstein 1978, 1981; DeNiro 1987; Chisholm *et al.* 1982; Schoeninger *et al.* 1983; Schoeninger and DeNiro 1984; Heaton *et al.* 1986; Keegan 1989; Schell and Ziemann 1989; Barnett 1994). The ranges I used for dietary categories were drawn broadly enough to reflect regional variations in isotopic values in plants and consumers, and while there may be consumers which do not absolutely conform to these ranges, it is fair to say that they represent conservative predictions which are generally used in paleodiet studies, such as those cited above.

While the rationale for using stable isotopes to reconstruct paleodiets is based on data collected on modern consumers, it still is important to confirm that Pleistocene consumers have isotopic signatures that conform to these predictions. Moreover, given my conclusion that Arctodus was carnivorous, I also wanted to explore whether stable isotopes could be used to distinguish the types of prey on which short-faced bears and other Beringian carnivores were feeding. Therefore, as part of this study I analyzed carbon and nitrogen isotope ratios in Pleistocene carnivores from Beringia that were unequivocal meat-eaters — *Panthera leo atrox*, *Canis lupus*, and *Homotherium serum*— and a carnivore that is omnivorous today — *Gulo gulo*. To gain further insight into how isotopes could be used to distinguish prey types, I analyzed carbon and nitrogen isotope ratios in six modern African carnivores with known differences in preferred prey — *Panthera leo*, *Panthera pardus*, *Acinonyx jubatus*, *Hyena hyena*, *Hyena brunnea*, and *Crocuta crocuta*. Techniques for extracting collagen and analyzing isotopes are identical to those found in the Methods section of Chapter 1. All isotope data generated from these carnivores and the bear data from Chapter 1 are compiled in Tables 23, 24, 25, and 26 of this appendix, and are depicted in Figs. 29 - 30.

The data from Pleistocene Carnivora (Fig. 29a) confirm that these known meat-eaters have isotopic signatures within the range predicted for modern secondary consumers in a C_3-dominated system. Even wolverines appear to have been purely carnivorous during the Pleistocene. Figure 29b shows how

the isotope values of short-faced bears are essentially identical to the other four meat-eaters, thus substantiating the conclusion that Arctodus consumed only animal flesh.

The analysis of African carnivores shows how carbon isotopes can be used to distinguish general categories of prey in many African ecosystems (Fig. 30). In sub-Saharan African ecosystems, woody plants use C_3 photosynthetic pathways to fix atmospheric carbon, while most grasses in these systems (especially savannahs) use C_4 pathways (Tieszen *et al.* 1979b). C_3 vegetation is significantly lighter in δ ^{13}C than C_4 vegetation, making browsing herbivores isotopically lighter in carbon than grazers (Tieszen *et al.* 1979a, Tieszen and Imbamba 1980, Ambrose and DeNiro 1986). Consequently, carnivores which consume browsers can be distinguished from those which consume grazers based on δ ^{13}C levels in their tissues. Typically in Africa, browsers and their predators will have δ ^{13}C collagen values around -22 to -17 ‰ while grazers and their predators will have values in the range of -12 to -7 ‰. Mixed feeders will have intermediate signatures (Ambrose and DeNiro 1986). These patterns are repeated in the isotopic signatures of the African carnivores tested in this study (Fig. 30a). All of the leopards had very low δ ^{13}C values, indicating that they consumed only browsers, which is consistent with the fact that leopards mostly hunt woodland herbivores. In the case of the four lions analyzed, three were strictly eating grazers, and one (from Serengeti) only hunted browsers. Cheetahs, spotted hyenas, and striped hyenas were mixed feeders. One cheetah ate only grazers, while the other either ate a mix of grazers and browsers, or ate prey which foraged on a mixture of grass and woody vegetation. The same pattern and conclusions can be drawn for spotted hyenas— three ate only grazers and one was a mixed forager. Of the two striped hyenas, one was eating browsers, while the other had an intermediate signal,[1] as did the single brown hyena.

Figure 30b demonstrates how no such separation of prey types can be made for Beringian carnivores because there is relatively little variation in their carbon isotope values. At present, it is unclear what, if any, meaning can be assigned to variation in δ ^{15}N values for Beringian carnivores. Trophic variation is an unlikely explanation, since all of these species most likely functioned as secondary consumers. Furthermore, the magnitude of variation for both carbon and nitrogen is essentially the same within and between species, which means we could not make any meaningful interpretation of the range of values (this conclusion about variation within and between species is based on visual inspection; no statistical analyses were deemed necessary because variation of a couple parts per mil within species is the norm for isotope data sets). Therefore, it would be spurious at this point to attach any ecological meaning to the variation depicted in Figs. 29b and 30b. A more extensive isotopic survey of Beringian mammals, including primary consumers, would be necessary before making specific interpretations about food web dynamics and ecosystem function.

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[1] This striped hyena was the only carnivore tested which was not from the African continent. It was collected in western Pakistan.

TABLE 23. Isotope values of bone collagen extracted from fossils of late Pleistocene Carnivora in eastern Beringia (all are from Alaska).

species	collection no.[1]	locality	bone type	$\delta^{13}C$	$\delta^{15}N$
Panthera leo	FAM 69148	Fairbanks Creek, Fairbanks	ulna	-18.12	8.32
Panthera leo	FAM 69149	Fairbanks Creek, Fairbanks	ulna	-17.83	6.42
Panthera leo	FAM 69151	Ester Creek, Fairbanks	ulna	-18.24	6.59
Panthera leo	FAM 69152	Fairbanks Creek, Fairbanks	ulna	-17.68	6.01
Panthera leo	FAM 69154	Goldhill, Fairbanks	ulna	-17.67	7.42
Panthera leo	FAM 69159	Goldstream, Fox	ulna	-17.93	6.48
Homotherium	A-182-5709	Engineer Creek, Fairbanks	ulna	-19.53	9.53
Homotherium	FAM 116841	Engineer Creek, Fairbanks	ulna	-1871	9.84
Homotherium	FAM 116839	Ester	unla	-19.13	9.33
Homotherium	A-200-4302	Little El Dorado Creek	cranium	-18.76	8.19
Canis lupus	A-255-6980	Goldstream, Fox	femur	-18.11	7.51
Canis lupus	A-255-6978	Goldstream, Fox	femur	-19.51	7.65
Canis lupus	A-453-2218	Cripple Creek, Fairbanks	femur	-19.63	5.72
Canis lupus	A-295-2149	Cripple Creek, Fairbanks	femur	-19.22	6.95
Canis lupus	A-197-8333	Ester Creek, Fairbanks	femur	-18.87	6.39
Gulo gulo	FAM 30798	Old Eva Creek, Fairbanks	cranium	-18.37	6.11
Gulo gulo	FAM 30795	Goldstream, Fairbanks	cranium	-19.30	7.44
Gulo gulo	FAM 30796	Ester	cranium	-18.45	7.68
Gulo gulo	FAM 30799	Cripple Creek, Fairbanks	cranium	-18.89	6.95

[1] FAM = Frick collection, American Museum of Natural History; A- numbers are field numbers of specimens in the American Museum of Natural History that do not have collection numbers assigned. Locality information is that listed on specimen tags.

TABLE 24. Isotope values of bone collagen (all skulls) extracted from modern African carnivores.

species	collection no.[1]	locality	$\delta^{13}C$	$\delta^{15}N$
Panthera leo	AMNH 85142	Serengeti	-19.60	11.94
Panthera leo	AMNH 52078	Congo	-8.34	7.57
Panthera leo	AMNH 52072	Zaire	-6.86	9.93
Panthera leo	AMNH 119870	Congo	-5.41	7.05
Hyena brunnea	AMNH 169448	Botswana	-11.69	10.59
Hyena hyena	AMNH 244436	west Pakistan	-13.89	12.77
Hyena hyena	AMNH 35431	unknown	-19.05	9.42
Crocuta crocuta	AMNH 83593	Botswana	-8.06	9.36
Crocuta crocuta	AMNH 114226	Tanzania	-6.95	9.54
Crocuta crocuta	AMNH 83592	Botswana	-8.54	9.49
Crocuta crocuta	AMNH 80621	Angola	-11.65	8.07
Panthera pardus	AMNH 120285	Kenya	-16.72	10.92
Panthera pardus	AMNH 52042	Zaire	-20.03	13.64
Panthera pardus	AMNH 169460	South Africa	-20.17	12.99
Acinonyx jubatus	AMNH 114517	"East Africa"	-6.81	11.44
Acinonyx jubatus	AMNH 161139	Ngorongoro.	-11.67	8.86

[1] AMNH = American Museum of Natural History

[2] localities are those listed by the collection records of the AMNH and may not reflect accurate modern country names

TABLE 25. Isotope values of bone collagen (all skulls) from two coastal and two inland populations of modern brown bears in Alaska.

collection no.[1]	locality	sex	age (years)[2]	$\delta^{13}C$	$\delta^{15}N$
Admiralty Island					
UAM 13789	Glass Peninsula, Doty Cove	F	10.4	-18.93	9.97
UAM 13791	Pybus Bay	M	7?	-17.04	12.16
UAM 13793	Pybus Bay	M	2.4	-16.91	13.50
UAM 13794	Chiak Bay	F	5.4	-20.04	4.37
UAM 13795	Gambier Bay	M	4.4	-17.77	8.87
ADFG 60	"Alpine Zone"	F	30.0	-21.06	1.13
Alaska Peninsula					
UAM 13943	Meshik River	F	2.4	-19.11	12.39
UAM 13947	Sandy River	M	5.4	-15.67	16.03
UAM 13948	Ilnik River	F	3.8	-18.48	8.91
UAM 13949	Meshik River	M	11.4	-15.59	12.95
UAM 13950	Port Heiden	M	13.8	-15.35	14.10
UAM 13953	Meshik River	F	15.8	-13.90	12.99
UAM 13961	Chignik Lake	?	1.8	-17.14	12.89
Interior					
UAM 2424	Fairbanks area	?	adult	-20.34	5.16
UAM 3394	Twelve Mile Summit	F	5 - 7	-19.17	3.94
UAM 14267	3.5 mile Steese Highway	F	6.5 - 7.5	-20.30	3.51
UAM 14268	Wood River, Alaska Range	M	4.8	-20.00	3.68
UAM 14269	Wood River, Alaska Range	F	14.9	-19.95	4.35
UAM 14270	Nenana	M	7.4	-20.51	4.70
UAM 14271	Bearpaw Creek	M	10.8 - 11.8	-18.47	8.70
UAM 14272	Tanana River, near Manley	F	6.6 - 6.8	-20.14	4.23
UAM 14274	Eagle Summit	M	13.8	-20.55	6.49
UAM 24077	Buzzard Creek, Totatlanika	M	1.5	-20.33	4.86
Brooks Range					
UAM 4825	Upper John River	F	> 5 ?	-19.25	2.86
UAM 9703	Siksikpik Creek	M	"old"	-18.75	5.03
UAM 9704	Masu Creek	M	"old"	-19.29	3.46
UAM 9707	Ukukminilagat	M	"old"	-19.16	4.48
UAM 9720	Inukpasukruk	F	5 ?	-19.81	6.37
UAM 9721	Ukikminilagat	F	4 - 5 ?	-19.65	4.90
UAM 9722	Kallutagiak Creek	M	5 - 6 ?	-18.75	5.45
UAM 9724	Anvik Creek	F	4 - 5 ?	-19.24	3.85
UAM 9725	Ukukminilagat	M	5 - 6 ?	-19.38	5.33
UAM 9726	Anvik Creek	M	5 ?	-19.97	5.86

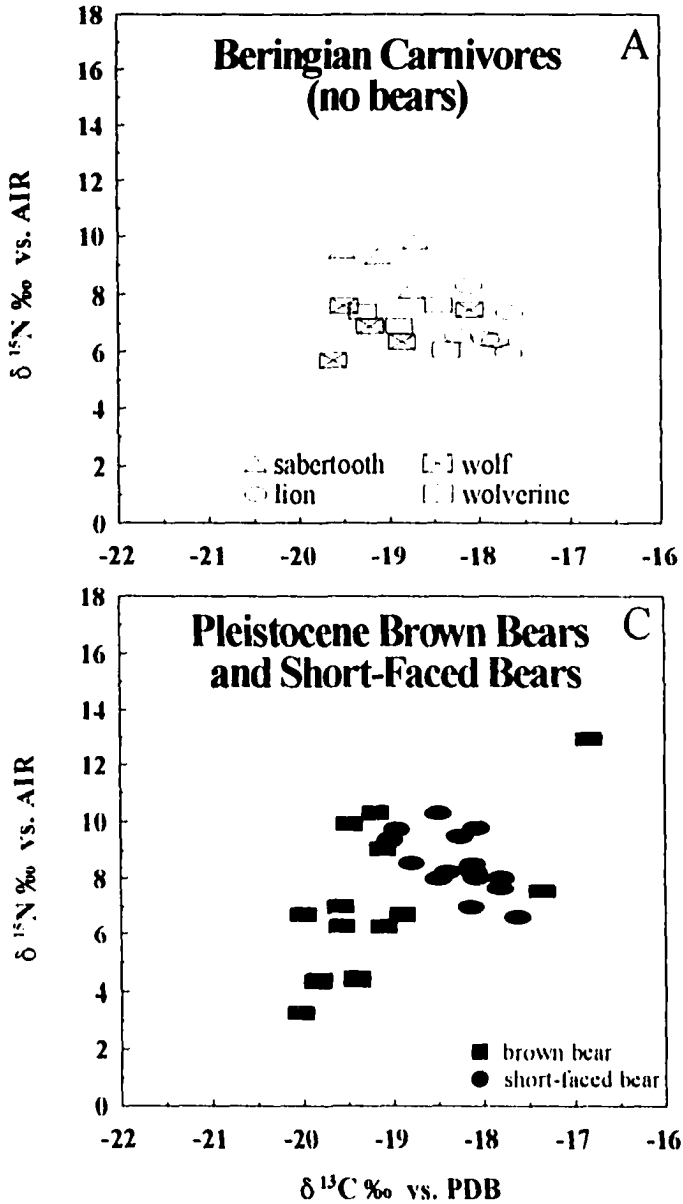
[1] UAM = University of Alaska Museum; ADFG = Alaska Department of Fish and Game

[2] ages based on number of premolar annuli (analysis by ADFG) or estimated (?) by suture closer, size, and tooth wear

TABLE 26. Isotope values of bone collagen extracted from fossils of late Pleistocene brown bears and short-faced bears in eastern Beringia.

species	collection no.[1]	locality	$\delta^{13}C$	$\delta^{15}N$
brown bear	NMC 29005	Sulphur creek, Dawson, Yukon	-19.57	6.29
brown bear	NMC 38279	Sixty Mile River, Dawson loc. 3, Yukon	-20.00	6.70
brown bear	NMC 47086	Caribou Creek, Dawson loc. 41, Yukon	-19.84	4.36
brown bear	NMC 35965	Hunker Creek, Dawson loc. 16, Yukon	-19.82	4.39
brown bear	FAM 95595	Goldstream Creek, Fairbanks, Alaska	-18.90	6.69
brown bear	FAM 95597	Goldhill, Fairbanks, Alaska	-19.59	6.98
brown bear	FAM 95598	Cripple Creek, Fairbanks, Alaska	-19.11	6.27
brown bear	FAM 95601	Cripple Creek, Fairbanks, Alaska	-20.03	3.30
brown bear	FAM 95610	Fairbanks Creek, Fairbanks, Alaska	-17.36	7.57
brown bear	FAM 95612	Ester Creek, Fairbanks, Alaska	-16.84	12.93
brown bear	AMNH 30421	Fairbanks, Alaska	-19.48	9.94
brown bear	AMNH 30422	Alaska (probably Fairbanks area)	-19.20	10.31
brown bear	AMNH 30780	Goldstream, Fairbanks, Alaska	-19.40	4.44
brown bear	"Colville"	Colville River, Umiat, Alaska	-19.12	9.07
short-faced bear	NMC 7438	Gold Run Creek, Dawson, Yukon	-18.49	10.31
short-faced bear	NMC 36236	Dawson area	-18.07	9.79
short-faced bear	NMC 37577	Hunker Creek, Dawson, Yukon	-18.96	9.74
short-faced bear	FAM 30492	Cleary (Fairbanks), Alaska	-17.80	8.04
short-faced bear	FAM 30494	Ester (Fairbanks), Alaska	-18.14	6.97
short-faced bear	FAM 95607	Ester Creek, Fairbanks, Alaska	-18.10	8.23
short-faced bear	FAM 99209	Ester (Fairbanks), Alaska	-18.12	8.54
short-faced bear	FAM 127688	Goldstream, Fairbanks, Alaska	-17.63	6.60
short-faced bear	FAM 127691	Engineer Creek, Fairbanks, Alaska	-19.04	9.37
short-faced bear	FAM 127699	Goldstream, Fairbanks, Alaska	-18.79	8.57
short-faced bear	AMNH 30494	Cleary Creek, Fairbanks, Alaska	-17.82	7.66
short-faced bear	A-37-10	Upper Cleary (Fairbanks), Alaska	-18.26	9.51
short-faced bear	A-197-2972	Cripple Creek, Fairbanks, Alaska	-18.13	8.37
short-faced bear	A-556	Cleary (Fairbanks), Alaska	-18.49	8.01
short-faced bear	L-gs-33	Goldstream, Fairbanks, Alaska	-18.39	8.25
short-faced bear	"Birch"	Birch Creek, 150 km NE of Fairbanks	-18.07	8.04

[1] AMNH = American Museum of Natural History; FAM = Frick collection, American Museum of Natural History; NMC = Canadian Museum of Nature, formerly National Museum of Canada; "Colville" and "Birch" are from private collections; A- numbers and L-gs are field numbers of specimens in the American Museum of Natural History that do not have collection numbers assigned.



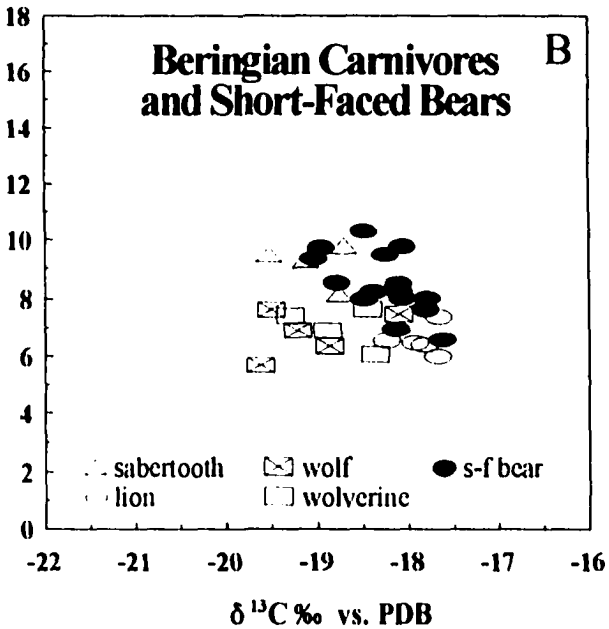


FIGURE 29. Carbon and nitrogen stable isotope values of bone collagen extracted from fossils of Beringian large Carnivora. *A* depicts values from known meat-eaters: sabertooths (*Homotherium serum*), steppe lions (*Panthera leo atrox*), wolves (*Canis lupus*), and wolverines (*Gulo gulo*). Isotopic signatures of these consumers conform with ranges predicted for terrestrial carnivores in a C3 system. Wolverines can be omnivorous today, but appear to have been purely carnivorous in the Pleistocene. *B* shows the same data plus values for short-faced bears and demonstrates the purely carnivorous diet of this bear. *C* is a simplified version of Fig. 2 of Chapter 1, and is provided to reiterate how Pleistocene brown bears and short-faced bears display significantly different trends in isotopic signatures and thus differed in their diets. In contrast to short-faced bears, Pleistocene brown bears had highly variable diets that included mostly vegetation, plus varying amounts of salmon and terrestrial meat (see Chapter 1).

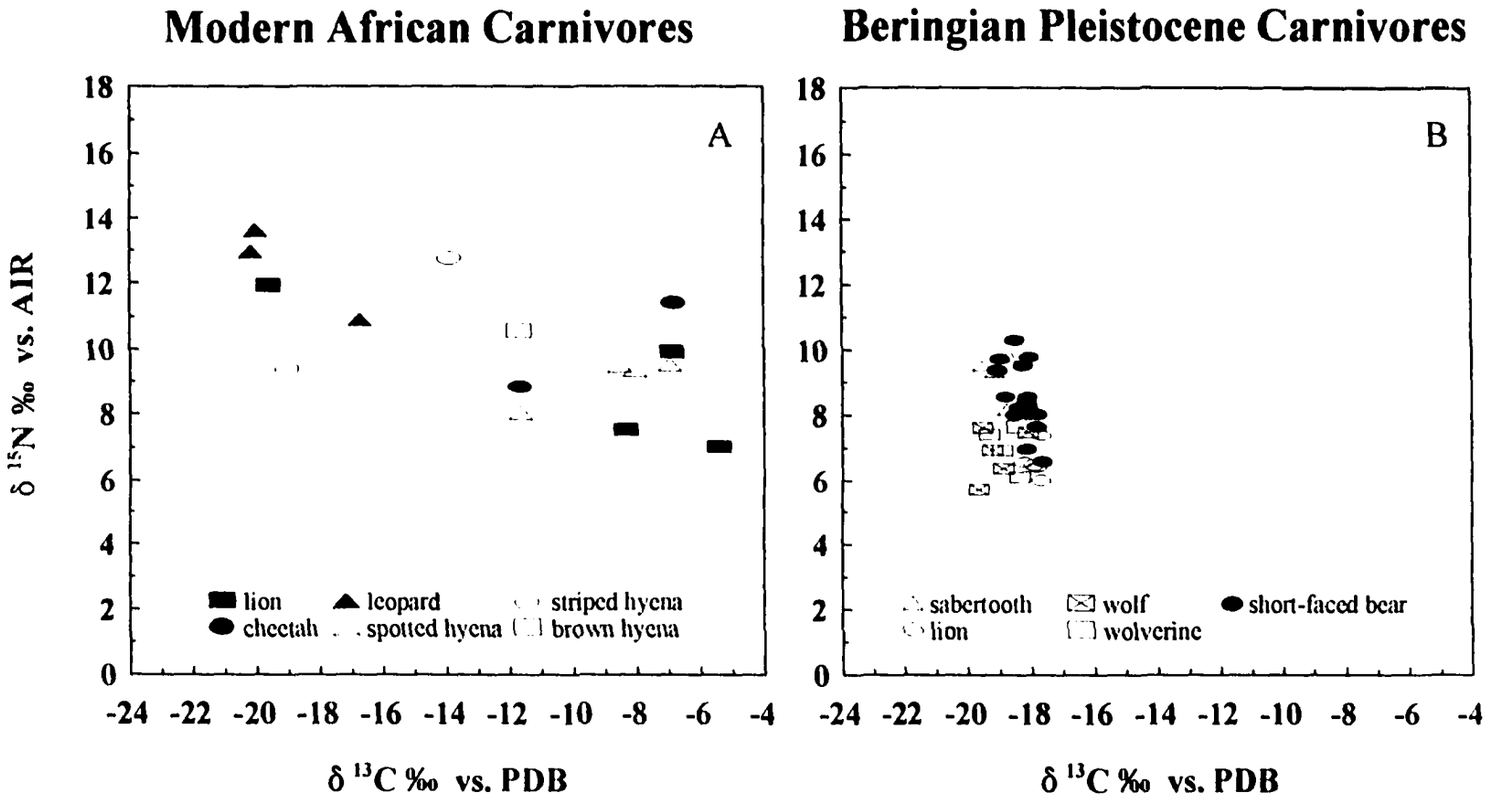


FIGURE 30. Carbon and nitrogen stable isotope values of bone collagen extracted from modern African large carnivores (*A*) compared to values derived from Pleistocene large carnivores in Beringia (*B*). African isotopic signatures demonstrate how $\delta^{13}C$ can be used to separate carnivores that are consuming browsing herbivores from those consuming grazing herbivores because in many African ecosystems woody plants (forage of browsers) use C_3 photosynthetic pathways and thus are substantially lighter in ^{13}C than grasses (forage of grazers), which mostly are C_4 plants in Africa. The narrow range of $\delta^{13}C$ values in Beringia shows that the ecosystem was a C_3 system, and that carbon isotopes can not be used to distinguish prey types in Beringian carnivores.

APPENDIX 2

LABORATORY PROCEDURES FOR EXTRACTING AND PURIFYING COLLAGEN FROM FOSSIL AND MODERN BONE

INTRODUCTION: *Overview of Technique and Theory*

This manual covers basic aspects of extracting collagen from modern or fossil bones for isotopic analysis. It also describes techniques for collecting bone samples. I wrote the manual for researchers, especially paleontologists and archaeologists, who may be unfamiliar with chemical laboratory protocol and require a step-by-step procedure for extracting collagen from whole bone. One of the main reasons for preparing this manual was that the techniques for extracting collagen found in the Methods section of published papers often are too terse and jargon-filled to be of much use for the non-specialist.

A brief review of bone composition and histology will be helpful for understanding the rationale behind the methods described in this manual. Fresh, dry bone is composed of around 25 - 35 % protein by dry weight, ninety percent of which is collagen (the other 10% is ostein, elastin, and other structural proteins)(Bloom and Fawcett 1968, Eyre 1980, Price 1989, Sillen 1989). The remaining 65 - 75% of bone dry weight consists of a complex heterogeneous crystal with an apatite-like structure, ($Ca[PO_3, CO_3]OH$), frequently referred to as bioapatite (Sillen 1989, Krueger 1991). The main constituent of bioapatite is hydrated calcium phosphate ($CaPO_3OH$), but a small percentage of its calcium atoms are substituted by various cations like magnesium and fluorine (Sillen 1989, Krueger 1991). Likewise, 2 - 5 % of the phosphate groups typically are substituted with carbonate (CO_3) (Krueger 1991).

Collagen, rather than the whole bone or the bioapatite fraction, is most commonly analyzed for stable isotope ratios because collagen is inherently less susceptible to irreversible contamination (Schoeninger and DeNiro 1982, DeNiro 1985, Chisholm 1989). Collagen also can be treated to detect and remove exogenous molecular contaminants more readily than can apatite. Moreover, collagen contains high percentages of both carbon and nitrogen, the two elements most commonly analyzed in stable isotope studies. Therefore, a major step in the laboratory procedure is to separate collagen from hydroxyapatite. Another important consideration for paleodiet studies is that bone collagen isotope values primarily reflect the isotopic ratios of consumed proteins, whereas carbonate values reflect the whole diet (Chisholm 1989, Sillen and Lee-Thorpe 1994). The turnover rate of bone in large mammals is around 7 - 10 years (Libby *et al.* 1964, Stenhouse and Baxter 1979), so stable isotope values from bone collagen represent multi-year averages of dietary and environmental conditions. Furthermore, no significant variation in isotopic

composition has been found among bone samples taken from different bones or different parts of bones (DeNiro and Schoeninger 1983).

Some researchers have attempted to use the carbon found in the carbonate of bioapatite for isotopic analysis, with varying and contentious degrees of success (see discussions in Sullivan and Krueger 1981, Schoeninger and DeNiro 1982, Nelson *et al.* 1986, Krueger 1991, Lee-Thorpe and van der Merwe 1991). The main objection to using bioapatite is that atoms in apatite crystals can be replaced by exogenous atoms without compromising its crystal structure, making it difficult to detect and remove contaminants (Schoeninger and DeNiro 1982).

In contrast, exogenous atoms cannot be directly substituted in the protein structure of collagen without causing a fundamental break-down of its structure (Chisholm 1989). Contamination of collagen can occur when the collagen macromolecule has already become degraded into smaller peptides and forms associations with exogenous organic molecules, usually from surrounding soils. In this case the "collagenous extract" no longer behaves chemically like collagen (Stafford *et al.* 1991). Therefore, poor-quality, contaminated collagen can be detected by simple assaying procedures. However, molecular contaminants such as soil humates, fulvic acids, and short-chain peptides also can adhere to (but not chemically combine with) intact collagen macromolecules (Stafford *et al.* 1988, Chisholm 1989). For this reason, collagen extraction from fossil bone should include treatments to remove these contaminants. Two complimentary treatments are described in this manual: 1) the widely used practice of soaking the collagen extract in a basic solution (KOH), and 2) separation by liquid chromatography using non-ionic, hydrophobic, styrene resins (XAD resins).

Not all fossil bone is suitable for collagen extraction and isotopic analysis, since most fossils probably will not retain enough intact (non-hydrolyzed) collagen to be analyzed. Even modern bone that has been left exposed to the elements may be leached of nearly all collagen. There are a number of analytical techniques and criteria that can be used for determining whether the extracted organic material is collagenous and suitable for isotopic analysis (these criteria are discussed by Stafford *et al.* 1988, 1990, 1991; DeNiro 1985, DeNiro and Weiner 1988). The most certain method is to analyze the extract's amino acid composition (versus a known collagen standard) using high performance liquid chromatography (HPLC). Usually, HPLC only is necessary for questionable samples or those that produce inconsistent results. An easier, yet reliable, way to confirm the collagenous origin of an extract is to assess its percent yield (weight of dry collagen/weight of bone analyzed) and its carbon:nitrogen ratio (C:N). Both methods should be used in conjunction with the other.

The maximum possible percent yield of collagen is about 30 %, based on its percentage in whole bone. When the yield is above 10%, the material extracted most likely is derived from original collagen; rarely, will material of < 5% yield produce accurate isotope values and its collagenous origin should be

considered suspect (Stafford *et al.* 1988). The reason for this is because usually there is a direct correlation between the quantity of collagen (percent yield) and its purity (Stafford et al 1988).

The C:N ratio of pure collagen is around 3.2:1 (Person *et al.* 1996). Ratios in the vicinity of 2.9:1 to 3.6:1 can be considered collagenous (DeNiro 1985, DeNiro and Weiner 1988) (soil organics that comprise most contaminants of collagen have much higher C:N ratios because they primarily are derived from decomposed plants). No extra analyses beyond mass spectroscopy need to be conducted to obtain C:N ratios, because they are easily calculated from data you will receive from the mass spectrometer readout. Percent yields also will be easy to calculate since the sample and the extracted collagen both will be weighed. However, both parameters can be used to screen which bones will be subjected to spectrographic analysis.

A good extract, then, is one that has both a high yield (> 10%) and an appropriate C:N ratio (around 3:1). In addition, a good quality extract of collagen can be identified by its appearance, and this manual will explain how to make qualitative assessments of the collagen's condition at various steps along the way. Because this manual is intended to present a "cookbook" method for the non-specialist, it will not discuss how to deal with collagen extracts of marginal quality. For more information on that subject see Stafford *et al.* (1988, 1990, 1991).

Since collagen is a protein that readily degrades after an animal dies and its bones are deposited, good collagen only can be recovered from well preserved bones of late Pleistocene to Holocene age. Some researchers have reported recovering original collagen peptides from Cretaceous dinosaurs (e.g., Bocherens 1988, Ostrom *et al.* 1991), but these were extracted from uniquely preserved fossils, and the results are still very contentious. The typical bones of Pleistocene mammals found in Alaska and the Yukon Territory can contain up to 100% of their original collagen, and are ideal for isotopic analyses. These bones are so exceptionally preserved because most have been buried in perennially frozen sediments. In fact, some still contain greasy marrow. Bones from desert and semi-desert caves often can have well-preserved collagen, too.

Layout of the Manual: The procedures that follow are laid out in seven sections:

1) Collecting Bone Samples
2) Sample Cleaning and Preparation
3) Demineralization
4) Gelatinization
5) XAD Preparation
6) Hydrolysis and XAD Extraction
7) Storing and Analyzing Collagen Extracts

Only the first four procedures are required to collect collagen from modern bone. All eight are necessary for fossil bone. Each section has four subsections:

1) Principles and Theory

2) Supplies

3) Step-by-Step Procedure

4) Notes and Hints

In addition, a sample data sheet is included at the end of this manual which indicates the type information to record at each step.

A few general comments apply to the overall procedure. First, the collagen being extracted for stable isotope analysis also can be ideal material for radiocarbon (^{14}C) dating. However, ^{14}C frequently is used as an isotopic marker in many biological research labs, especially those studying plant and animal physiology, soil microbes, and limnology, and it is used in biomedical research labs. ^{14}C is very mobile and "sticky," and quickly becomes transported throughout the buildings that such labs are housed in simply by people who come in contact with it. If collagen samples are being collected for radiocarbon dating (even if this is a possibility in the future), care should be taken to set up the facilities for extracting collagen in an area free of elevated ^{14}C levels. Minimally, this means conducting the work in a building that has never had a history of ^{14}C use. In any suspect cases, or when a building's history can not be ascertained, the researcher should perform a bench-top wipe-test to determine if elevated levels of ^{14}C are present in his/her laboratory space. The wipe-test is simple to conduct, but will require the assistance of a technician who is trained to perform the necessary scintillation counts.

Similarly, collagen extractions should be performed in a very clean work space, and glassware and apparatuses must be kept absolutely clean to avoid contamination by organic materials which may introduce carbon and nitrogen into the sample (this is especially important if the collagen is to be used for ^{14}C analysis). All glassware (pipettes, culture tubes, etc.) should be new and combusted in a 550° C muffle furnace for 6 hrs in order to burn off carbon residues and other organics. Glassware should be wrapped in aluminum foil for protection when it is combusted and during storage. Glassware and other supplies should be stored in a dust-free environment such as a plexiglass desiccator cabinet. All chemicals used throughout the procedure should be reagent-grade. Water must be filtered, purified by reverse osmosis, and be reagent-grade.

The procedures call for the use of many pipettes and culture tubes, and I recommend using 5 $^3/_4$ inch disposable Pasteur pipettes and 16 X 100 mm culture tubes, although the size of the latter will vary depending on the average size of bone being processed. Caps for these tubes should be Teflon (PTFE) lined. On average, 2 culture tubes and two caps will be used-up per sample. Numerous pipettes will be used.

In addition to the supplies listed in each section, a few pieces of general laboratory equipment are required. These include a centrifuge (with proper-sized adaptor), hotplate with hotblock and thermometer, lyophilizer, muffle furnace, analytical balance, a vacuum pump and a refrigerator. Loose supplies on hand should include: vacuum hose, hose clamps, tape (colored laboratory and clear Scotch-type), marking pens, stainless steel chemical spatula, glass stirring rods, clean glass beakers, aluminum foil, Kimwipes, pH paper, new squeeze bottles, and a small rubber pipette bulb.

Finally, I recommend running samples through the extraction procedure in batches of about 10 - 16 samples. This is about as many as can be processed conveniently at one time without facing procedural backlogs and bottlenecks. Mainly, this is because most of the apparatuses being used, such as the centrifuge and lyophilizer, have limited numbers of ports. Therefore, batches of more than 10 - 16 samples tend to get split up anyway because their processing at any given step cannot be completed simultaneously.

1. COLLECTING BONE SAMPLES

Principles and Theory

What type of bone should be sampled: Bone from nearly any skeletal element can be used for collagen extraction if necessary, but solid compact bone will give the best results and is much easier to deal with in subsequent laboratory procedures. Unlike spongy bone, compact bone has few vacuities for macroscopic contaminants to be lodged in. Likewise, the voids in spongy bone (in modern samples) usually contain old, dried soft tissue (blood vessels, lipids, hemopoietic tissues) whereas compact bone is mostly void of macroscopic soft tissues. Since blood, lipids, and other soft tissues usually have isotope ratios different than bone collagen, they need to be separated from the bone. In addition, spongy bone from fossils often contains sediments or organic material, which should be avoided. For these reasons, it is highly desirable to sample a piece of solid-looking, ungreasy, compact bone from both modern and fossil bones.

Where to Sample on the Bone: On a long bone, the ideal place to sample is on the shaft, since compact bone is thickest there. Try not to sample from the ends of a long bone in order to avoid spongy bone and so that critical articular surfaces are not disturbed for other studies. On a skull, ideal spots to sample are the ventral surface of the mandible and anywhere along the zygomatic arch. These are locations where compact bone is thickest. The thin dermal bones of the skull are not preferred because they have an internal spongy layer with many vacuities and soft tissue residues.

Unfortunately, the preferred sampling points on long bones and skulls leave obvious scars on specimens, but unless they are to be used as display pieces, the increased quality of the bone sample usually is worth the small cosmetic blight. As long as important points of muscle attachments and

articular surfaces are not destroyed, the scientific value of the specimen is not substantially reduced by the sampling procedure.

When a display specimen is sampled, or when minimal destruction of the specimen is necessary, alternative sampling locations can be used. On skulls, bone can be collected from inside the braincase, usually from the tentorium, although this interferes with future potential for making brain endocasts. Often, there are small piece of bone lying loose in a specimen's storage box. These can be taken for analysis, although its impossible to be absolutely certain the pieces actually come from the associated specimen. Skulls are usually the most valuable pieces in a collection, but sometimes they are accompanied by other skeletal elements from the animal. There is no evidence that isotope ratios differ between different bones, so it is preferable to leave the skull alone and sample another bone. One of the best sampling points is along the ragged ends of broken bones, since the bone can be easily inspected and minimal cutting and damage is done. However, before sampling from a broken edge, one first must determine that the area does not provide critical taphonomic or archaeological information that would be destroyed by sampling, such as breakage from prehistoric human use.

How Much Bone to Collect: Ultimately, about 2 mg of pure, dry, collagen extract is needed for isotopic analysis on a mass spectrometer such as the Europa 99 at the Institute of Marine Science's stable isotope lab at the University of Alaska Fairbanks. Theoretically, this means that only 8 mg of whole bone need be collected, assuming a 25% collagen content. This proves to be unrealistic because 8 mg of bone is too small to practically handle during subsequent laboratory procedures (i.e. smaller amounts of collagen become mere residues on glassware), and because there is inevitable loss of collagen during transferring and washing. Realistically, a better goal to end up with a minimum of 20 mg of pure collagen, and preferably about 50 to 100 mg. It is recommenced that 1 to 2 grams of whole bone be collected, but as little as 0.3 to 0.5 grams will work. Ideally, half of the collected bone should be curated as a voucher and for future analysis, and the other half used for collagen extraction. Using less than about 0.3 g of whole bone for extraction will require special modification to the procedures in this manual. It will become easier to successfully extract useable amounts of collagen from small bone samples after first gaining proficiency in the extraction procedure.

Supplies

- Dremmel-type rotary tool with cut-off blades, grinder head, and other tips
- Kimwipes or similar paper wipes
- jewelers saw (optional; possible alternative to Dremmel)
- pliers (optional, but very handy)
- sample vials
- tape and sharpie marker
- caliper, tape, etc... if specimen needs to be measured too
- scale for weighing sample
- sample data sheets

Step-by-Step Procedure

1- Place a new cut-off wheel on the Dremmel and clean the wheel with water and a Kimwipe.

2- Choose the area on the specimen to be sampled following guidelines above. Clean the sampling area with a dry Kimwipes.

3- Cut a rectangular piece of bone from specimen. On Zygomatic arch, make two parallel cuts about 1.5 cm long and 2 to 3 cm apart on the ventral surface, perpendicular to the arch. Then connect these two cuts with a third, perpendicular cut. On a long bone, the procedure is similar, except that a fourth cut must be made to complete the rectangular cutout. The easiest sampling is done on a long bone with a broken shaft, but take note of the earlier caution about destroying informative breakage surfaces.

4- Place sample in a new, clean storage vial and label (do not write on the bone). If labeling tape is used, also label the glass, itself, since labels can fall off.

5- Start a sample data sheet for the sample by assigning it a lab number and recording data about the specimen, such as date and location of collection. Also note the skeletal element sampled. It is especially important to note the condition of the bone (i.e., is it greasy, dense, leached, stained, covered by preservative, etc. ?) and record the weight of the sample.

5- Ideally, change the cut-off wheel between samples, but as a minimum, clean it with water and a Kimwipes.

Notes and Hints

1- Cutting the bone with a rotary tool produces dust and a strong odor, so perform sampling operation under a fume hood or outdoors. Museum personnel should be notified of this byproduct of sampling.

2- Cutting wheels break often, so have plenty available.

3- Cutting procedure will not always result in clean, connected cuts, and often it will be difficult to complete a cut in all planes. Therefore, use a pliers to break off samples that can not be completely cut.

4- Scintillation vials make good storage containers for samples. Avoid plastic bags since they tend to rip from the sharp edges of bone samples.

2. SAMPLE CLEANING AND PREPARATION

Principles and Theory

In this procedure, the bone will be cleaned and prepared prior to the main extraction procedure. The goal is to remove as many macroscopic contaminants as possible, including dirt, varnishes, glues, and a host of other patinas and residues on the surface of the bone (such as algae growth). The procedure

begins with physically washing and scraping the specimen, followed by sonication (which "vibrates" particles off the bone) and a series of chemical washes. Acetone and alcohol washes (ethanol and methanol) remove varnishes, shellacs, and glues. These contaminants are most likely encountered in older collections of fossil bone, but many modern bones in museums have glues and preservatives, which must be removed. Finally, modern bone must be degreased with a series of chloroform treatments.

Supplies

-combusted culture tubes with screw-on caps [1]
-chloroform
-filtered R.O. water
-sonicator (not absolutely necessary)
-Dremmel-type tool with sanding head
-rubber gloves
-ethanol
-acetone
-methanol

Step-by-Step Procedure

Initial Procedure for all Bone

1. Using Dremmel with sanding head, grind off the outer cortex, or rind, of the bone. This is the area likely to contain the most contaminants. Also, it is best if cancellous areas are removed at this time, since they tend to trap dirt, remnant soft tissue, and other contaminants. This should leave you with a nice solid piece of bone.
2. Place bone in culture tube and clean with a few rinses of water.
3. Place tubes containing samples and clean water in the sonicator bath for about 1 minute. Examine to see if particles are being sonicated off.
4. Soak bone for about 8 hrs each in ethanol, methanol, and acetone. Any order is fine, but you should wash the sample with water between alcohol and acetone treatments. If you notice a strong reaction between one of these chemicals and a preservative on the bone, then change the solution a few times during the 8 hr period.
6. Wash the sample well with water so that no chemical residues remain. Fossil bone is now ready for demineralization. Modern bone must be degreased first.

[1] Clean, combusted culture tubes should be used throughout the extraction procedures in this manual. To combust tubes, loosely wrap about 24 in an aluminum foil "jacket" and place in a 550° C muffle furnace for at least 6 hours. Combusting the tubes removes carbon contaminants. Screw-on caps can not be combusted, so only new caps should be used.

Degreasing Modern Bone

1. Soak bone samples in chloroform for a minimum of two times at 8 hrs each. Very greasy bone may require additional treatments. This procedure should only be conducted under a fume hood (see note below)
2. After treatments, air-dry the samples under a fume hood to evaporate residual chloroform. Then, before proceeding to demineralization, rinse the samples well with numerous washes of clean water.

Notes and Hints

1- Important Note: Chloroform is a known carcinogen and is very volatile, so always wear gloves and work under a hood. Waste chloroform should be stored in containers for collection by hazardous waste personal. It must never be poured down the drain.

2- When soaking bone in alcohol and acetone, remember that each of these solvents dissolves a different class of preservative. If it is observed that one solvent has a strong effect (i.e., it produces a milky film on the edge of the bone) then provide the sample with numerous soakings of this solvent and keep the solvent fresh.

3. DEMINERALIZATION

Principles and Theory

The first and main step of collagen extraction is to separate the collagen and mineral (bioapatite) portions of the bone. This is done by soaking the sample in weak hydrochloric acid (HCl) at low temperatures. This dissolves the bioapatite and leaves behind an insoluble fraction that is mostly collagen. However, the collagen fraction also contains other minor bone proteins and miscellaneous tissues fragments. The insoluble ("collagenous") fraction should be a flexible ("rubbery-feeling") pseudomorph, which will look like a translucent copy of the original bone. It is important to note that a solution of HCl which is either too strong or too warm can hydrolyze and thus destroy the collagen, in addition to the hydroxyapatite. Thus, the goal of the demineralization step is to dissolve the bioapatite without hydrolyzing the collagen.

Before demineralization, weigh the entire sample and then weigh the piece that is processed and record both weights on the sample data sheet. Preferably, enough bone was collected from the original specimen so that half can be curated as a voucher and half can be processed for collagen.

Supplies

- clean, new, combusted culture tubes with caps and storage rack
- 6N HCl in clean, new squeeze bottle or burret
- 5 % KOH
- filtered R.O. water in clean, new squeeze bottle

Step-by-Step Procedure

1- Weigh the sample that was cut from the specimen and record its weight

2- Cut a sub-sample of the original sample. The sub-sample will be used for demineralization. It is important to record the weight of the piece actually being demineralized because this weight will be used to calculate percent yield.

3- Place the bone sub-sample in a culture tube and fill the tube about 3/4 full with water

4- Add about 1.0 - 2.0 ml of HCl (equivalent to one good squirt from the squeeze bottle) and set a cap loosely on the culture tube (demineralization liberates CO_2 gas which will burst the culture tube if the cap is closed tightly).

5- Place rack with samples in refrigerator and monitor bubbling by checking every few hours. When the rack is shaken, bubbles should rise from the samples. Also, if allowed to sit for 5 - 10 minutes at room temperature, the samples should begin bubbling. This is CO_2 being released from the reaction of HCL with the carbonate of bioapatite.

6- Recharge the acid as needed over the first 12 - 24 hours in order to maintain bubbling (but samples should not actively bubble when cold). As more acid is added, phosphate salts will begin to saturate the solution and precipitate out, so the water should be changed about every 24 hours (next step).

7- After about 24 hours, decant the solution and add fresh water and a fresh charge of HCl. Repeat this every subsequent 24 hours (times need not be exact— the goal is just to keep salts from accumulating).

8- Demineralization is complete when no more bubbles can be liberated from the bone, and all that remains is a translucent pseudomorph. NOTE: the complete process can take 7 - 10 days, depending on the size, and especially thickness, of the bone.

9- After demineralization is complete, rinse and wash the bone with the jet-action of a squeeze bottle stream to remove other tissues that may be adhered to the pseudomorph (but be gentle). Rinse numerous times to neutralize the acid. This is especially important if the samples are to be stored before proceeding to the gelatinization step (samples should always be stored in under refrigeration).

10- *Base Treatment (Fossil Bone Only):* After demineralization and acid neutralization, fossil samples are soaked in KOH to partially remove humic and fulvic acids. Place about 5 - 10 ml of water in the culture tube with the sample and add about 0.5 ml of 5 % KOH solution. Allow to soak at least 8

hours, and monitor color change in the sample and the solution. Often, the KOH treatment will make the sample visibly whiter, while the solution becomes brown. This is good and means that the treatment removed some contaminants. Samples which are noticeably affected this way should be given a second base treatment. After treatment, rinse samples to neutral pH with numerous water washes. (Chisholm 1989 reviews reasons for and against subjecting collagen to a base treatment. It is debatable whether base treatments effectively remove more fulvic and humic acids than does the acid treatment during demineralization, and base treatments may not be a necessary step if XAD extractions are performed.)

Notes and Hints

1- Long, skinny pieces of bone demineralize fastest because acid can readily reach the interior portions. Blocky pieces demineralize slower and tend to leave portions in the center that do not completely demineralize. The translucency of the bone will be a good indicator of this problem: portions which have not demineralized will appear opaque.

2- Look for calcium and phosphate (white) salts accumulating around the bone and on the bottom of the culture tube. If these are present, change the solution more frequently.

3- The key to this step is to dissolve the hydroxyapatite without hydrolyzing the collagen. The latter will happen if the samples are not kept cool and the acid is too strong. Still, experience has shown that it is difficult to add too much acid, and not adding enough will add days to the processing time, so do not be too hesitant about adding more acid in order to keep the demineralization process going.

4- If it is desirable to cut down significantly on processing time, the sample can be powdered or cut into small pieces. Powdered samples will be totally demineralized in about 24 hours. However, powdering is not recommenced because powdered material is difficult to wash and transfer. It is especially difficult to decant solvents from a tube containing powdered-bone because the powder floats. Also, powdering tends to reduce the percent of collagen recovered for three reasons. First, much bone is lost in the powdering process. Second, the increased surface area of the powder versus whole bone means that more collagen is likely to be lost to unintentional hydrolysis. Third, powder does not transfer well and some gets left behind on glassware. Likewise, some is bound to be lost through decanting (an alternative to decanting is to pipette solvents from the culture tubes).

4. GELATINIZATION

Principles and Theory

The purpose of the gelatinization step is to separate the collagen from other proteins and organic compounds which remain after demineralization. The procedure utilizes the fact that collagen will denature and dissolve (but not hydrolyze) when warmed in a slightly acidic solution, whereas other proteins tend to form precipitates under such condition (Gustavson 1956, Häkansson 1976). Therefore, keep in mind that in this procedure, the supernatent is collected and the insoluble portion is discarded, unlike the demineralization step. To gelatinize the collagen, the sample is placed in a culture tube with a few milliliters of water, to which a small amount of HCl is added until the pH is between 3 and 4. All air is evacuated from the culture tube with an inert gas and the tube is tightly capped. This is done to prevent fragments of the collagen molecule from forming oxides when heated; these will precipitate out of solution and reduce collagen yield. The sample is heated for 2 to 6 hours, or as long as it takes to dissolve a satisfactory amount of collagen. I say satisfactory because some samples may not totally dissolve and further heating may hydrolyze the collagen which did dissolve. In this sense, the goal is to maximize the amount of "good" collagen that is recovered. After dissolution, the sample is centrifuged, and the supernatent (collagen) is separated, lyophilized, and weighed. If the collagen is from modern bone, it then is ready for isotopic analysis. If the collagen is from fossil bone, the collagen should be further treated by XAD extraction in order to remove persistent contaminants.

A good product at the end of the getalinization stage (i.e., dried collagen) should look whitish and be acicular. If the dried collagen is brown and dense, it has been slightly hydrolyzed by overly rigorous acid treatments. If the collagen extract does not dry during lyophilization, it has been severely hydrolyzed. Any collagen that can be dried is suitable, but its appearance is indicative of how well the extraction procedure went (in cases of questionable bone, a poor-looking extract can be a sign of poor collagen preservation).

Supplies

- culture tubes with Teflon screw-on caps
- 3 cc to 5cc syringe with plunger and lure-lock fitting
- 50 mm Teflon syringe filter disks with lure lock fitting and 45μ pore size (recommended: Millex-HV, 50 mm with 0.45 micron Teflon filter, catalogue # SLHV025NS)
- aluminum hot block bored to hold culture tubes (or similar devise)
- hot plate
- thermometer
- combusted pipettes
- tared scintillation vials
- round glass filter disks (recommended, 5.5 cm

Whatman's glass filter disks; do not use paper filter disks) and tape
- pH paper
- centrifuge
- lyophilizer
- tank of compressed inert gas (nitrogen or helium) fitted with Teflon tubing (~5 mm O.D.)
- 6N HCL in single-drop squeeze bottle (less concentrated HCL even better)
- filtered R.O. water
- liquid nitrogen (optional)

Step-by-Step Procedure

1- Rinse the demineralized bone with water to remove any contaminants/particles liberated by the demineralization process.

2- If bone was base-treated, rinse well to neutral pH.

3- Place as little water in the culture tube as necessary to dissolve the collagen (this amount will vary, but start with about 4 - 5 ml). Be conservative because this water will need to be lyophilized later.

4- Acidify the solution to a pH between 3 and 4. This probably will require adding only one drop (.05 ml) of HCL from the squeeze bottle. Often, this will make the pH too low. To raise it, add and then decant some water. Verify that pH is 3 - 4.

5- Evacuate air from the culture tube. To do so, place a combusted pipette over the Teflon tubing attached to the compressed gas regulator. Turn on gas very slightly and bubble gas into the culture tube to evacuate air from the chamber, using the pipette as a nozzle. Bubble the gas directly above the water surface for about 15 seconds. Pull out the pipette and quickly seal the tube tightly with a Teflon cap.

6- Place tubes in aluminum hotblock and heat at 100° C for as long as it takes to dissolve the collagen, but no longer (heating to 100° C will require pre-heating the hotblock to about 110° C). Dissolving the collagen usually will take between 1 to 4 hours. Check the samples about every 15 minutes and note the rate of dissolution. Most of the collagen will dissolve in about 0.5 - 1.0 hour. Each sample will dissolve at its own rate and must be treated individually. For some samples, not all of the collagen will dissolve. When the rate of collagen dissolution plateaus for a sample, remove it from the hotblock (but do not let it cool down; proceed to the next steps while other samples continue to heat). It is important to avoid overheating or heating for too long because this will begin to hydrolyze the collagen, making it difficult to lyophilize.

7- While samples are heating, prepare syringes and syringe filters by connecting them at their luer-lock fittings. Run a few milliliters of water through them to rinse out particulates. Position the syringe/filter unit on top of a tared scintillation vial so that the filter's outlet flows into the vial.

8- When samples are done heating, centrifuge at ~2000 RPM for 3 - 6 minutes. Pipette the supernatent into a syringe/filter unit and pass it through the filter using the syringe's plunger. Collect the filtrate in the scintillation vial, and label vial with specimen number. If it is important to retrieve all of the collagen (such as when a very small sample was used), the pellet left in the culture tube can be rinsed with a small amount of water, which then is passed through the syringe and filter and collected in the vial.

9- Place a glass filter disk over the top of the vial and secure with tape. The filter disk acts as a cover to keep out contaminants, yet allows the sample to dry in the lyophilizer (water vapors will pass through the filter disk). Do not use paper filters, as they are a likely source of carbon contamination.

10- Lyophilize the samples. Normally, this will take 8 - 12 hours for a 4 ml sample. If samples cannot be lyophilized immediately, store in a freezer.

11- Measure dry weight and calculate percent yield as: *collagen dry weight ÷ bone sample weight X 100.*

Notes and Hints

1- It is vital to maintain the pH between 3 - 4 (and closer to 4 is better than closer to 3). If too acidic, the samples will hydrolyze when heated and then will not lyophilize well. Use lots of pH paper to make sure the pH is correct (recall basic chemistry protocol and do not dip pH paper into the sample; instead, pipette out a small amount of the solution using a clean pipette and add a drop to the paper).

2- The temperature of the hot block can range between 95 - 105 ° C, but should not exceed 110 ° C.

3- If heating does not dissolve all of the collagen, the remainder can be retreated as per steps 3 - 5 and reheated. If it is common that the samples do not fully dissolve, then you are not using enough water in step 4.

4- It will take experience to learn how much water to add for gelatinization. In actuality, adding too much water only should be a concern only when dealing with a weak lyophilizer, or when lyophilizing is a time-bottleneck (but weak lyophilizers are not uncommon). If you have a strong lyophilizer (i.e., good pump and no leaks) which can dry many samples simultaneously, then it is best to error by adding slightly more water than necessary, in order to assure that the maximum amount of collagen dissolves.

5- Samples lyophilize faster if they are semi-frozen into a viscus "slush" first, and then swirled around to coat the side walls of their vials (after being swirled, the samples must be frozen immediately, otherwise they will settle to the bottom of the vial again). This increases the surface area available for the sublimation process. It is a good practice to do this for all samples, but it is especially important for those with large volumes of water. To semi-freeze and swirl a sample, two alternative procedures are offered: either dip the vial in liquid nitrogen for a few seconds and then swirl, or place the vial in a freezer and swirl it before it freezes solid (a good freezer for this purpose is the condenser of a

lyophilizer, since it reaches very cold temperature, near -70 · C; other freezers are less desirable because they freeze the samples too slowly.). The liquid nitrogen procedure is preferable, since it is quicker and less hassle.

5. XAD PREPARATION

Principles and Theory

XAD resins are small beads of a nonionic, hydrophobic styrene polymer. Microscopically, the beads are comprised of many smaller beads, forming a highly porous reticular structure with a large surface area.[2] To remove contaminants adhering to the collagen, the collagen is hydrolyzed in a strongly acidic solution and passed through a bed of XAD resin. The strong acid functions both to hydrolyze the collagen and to saturate negatively charged sites on all peptides with hydronium ions, which reduces their polarity. Non-polar hydrophobic contaminants that are smaller than the collagen peptides will be adsorbed (retained) by the reticuli of the resin, while the collagen flows through as an eluate, mainly by virtue of its size. The spent columns of XAD can be curated as a voucher for the contaminants that were extracted. These contaminants (mainly fulvic acids) can be recovered for analyses by desorbing them from the column. I do not discuss the process for collecting or analyzing contaminants (for such procedures, see Stafford *et al.* 1988).

The laboratory procedures in this step are twofold. First, the XAD resin, which is shipped and stored dry, must be washed and hydrated using special procedures. This involves cleaning and rinsing the resin with a non-polar solvent, usually acetone, which penetrates the fine reticular surface. A polar solvent like water would be prevented from entering reticuli because of the resin's hydrophobic structure. Second, water is added to the resin in numerous washes to dissolve and remove the acetone. Then, a strong HCL solution is added. XAD resin is stored in this acid solution. After the XAD is hydrated, columns with resin beds are prepared. The prepared columns are basically syringes with · 2 cm of hydrated XAD resin compacted between two glass-fiber frits. I recommend preparing the XAD and the extraction columns before or during the subsequent hydrolysis step, so they are available immediately as needed.

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[2] XAD resins are a broad category of resins made of various polymers and come with a variety of pore sizes and surface structure. Stafford *et al.* (1988) have determined that XAD-2 is best suited for collagen purification. Its styrene construction is resistant to acid decay, and its pore size of 90A is small enough to allow collagen peptides to flow through, yet large enough to retain fulvic acids

Supplies

- Amberlite XAD-2 Analytical Grade Resin (0.1 - 0.2 mm beads) purchased dry in 25g bottles.
- syringe-type columns (4 cc) with two removable frits (recommended: Alltech Extract Clean Filter Columns, 4 ml, catalogue # 211104)
- filter disks (recommended: Millex-HV, 50 mm with 0.45μ Teflon filter, catalogue # SLHV025NS)
- acetone (clean analytical grade)
- filtered R.O. water
- Normalized HCL (around 6 *N*)
- small separatory funnel, about 150 ml (plastic serum vials or other sealable container will work too)
- disposable combusted pipettes
- centrifuge (if serum vials are used)
- test tube of almost any size to catch waste HCl

Step-by Step Procedure

A. Hydrating XAD Resin (see technical bulletin from Rohm and Haas and Stafford et al. 1988)

1- Transfer the portion of resin to be hydrated into a separatory funnel or serum vial (hydrated resin can be stored for about 6 months, so extra resin can be prepared at this time). Add enough acetone to make a slurry— just enough to soak the resin. The resin is highly charged with static electricity, so sometimes it is easiest to add acetone straight to a powdered aliquot (or into the container in which the XAD is stored) and transfer it wet to the funnel or vial with a pipette. Acetone is used instead of water because a non-polar solvent is required to make a slurry out of the non-polar resin.

2- Once the slurry is transferred to a separatory funnel or vial, the acetone must be rinsed out with numerous (6 - 10) water washes. When water is added to the slurry, a bilayer will form with resin on the bottom and water on top. Let the solution soak 15 minutes between washes. This extracts acetone from the resin (the acetone dissolves in the water) and allows a well-defined bilayer to be formed. If a separatory funnel is used, the bottom stopcock is opened between washes to drain water. Add new water and repeat the washing/draining procedure. If a serum vial is used, the water must be pipetted from the bottom layer (this is the reason for using a separatory funnel). Centrifuging the serum vial during each wash also assists the separation between water and resin.

3- After the last water layer is pipetted off, add a volume of 6N HCL that is about twice as voluminous as the resin bed. A bilayer will form, but now the resin will be on top. Final molarity should be between 1.0 to 6.0. Resin is now ready for use or storage for up to 6 months.

Notes and Hints for Hydration

1- Once resin is hydrated, it should not be allowed to dry out. If it drys out, the rehydration procedure will need to be repeated.

2- After about 6 months of storage, the resin will degrade and turn light brown.

3- Because of the resin's static charge, it adheres strongly to whatever touches it. Therefore, some resin will be lost just by pipetting during the washing process. This is avoided by using a separatory funnel instead of a serum vial because water is drained out from the bottom of the funnel (however, a serum vial is a more desirable storage container, and hydrated resin can be transferred to one after final preparation).

B. Preparing Columns

1- Multiple columns can be prepared simultaneously

2- Place one frit in the bottom of the column

3- Pipette enough XAD slurry into the column so that there will be about a 1.5 - 2.0 cm bed of resin when it is compressed.

4- Add the second frit and compact the resin by pushing the frit down with the back of a pipette. Acid solution will be forced out the bottom of the column, so be prepared to receive the acid in a beaker or test tube. The resin should be compacted slowly and evenly. The goal is to produce a tight resin bed with no air pockets.

5- Place a filter on the bottom of the syringe column.

6- The column and filter should be rinsed by placing two bed volumes of 6 N HCL solution in the column and letting it flow by gravity through the resin and filter (flow will be slow; takes about 10 minutes). Gravity flow sets up a vertical stratification in the resin bed by bead size. Flow will have to be initiated using a pipette bulb which has been placed over the top of the column (squeezing the bulb forces the HCL through the resin and filter). Capture HCL effluent by placing a test tube or similar receiver under each column.

7- When all HCL has drained, the column is ready for use. Columns can be stored for up to 2 weeks by sealing each end with parafilm. Before use, run one bed volume of HC through each column.

6. HYDROLYSIS AND XAD EXTRACTION

Principles and Theory

Fossil collagen samples are subjected to this addition step where persistent organic contaminants are removed by liquid chromatography using XAD resins. In all previous steps, care was taken not to

hydrolyze the collagen. In this step, the collagen must be hydrolyzed in strong acid in order to pass through the XAD resin bed. Acidifying the collagen also depolarizes exogenous small-chain peptides and other contaminants so they will be retained in the reticuli of the XAD resin during extraction (see previous step).

Procedurally, a small amount of strong HCL is added to the dried collagen and the solution is heated in a sealed culture tube. This dissolves and hydrolyzes the collagen. As with the gelatinization procedure, the culture tube is evacuated with inert gas to prevent collagen-derived oxides from precipitating. Precipitates are more likely to form in this step than during gelatinization because the collagen is hydrolyzed into peptide chains and even some individual amino acids. These are more likely to oxidize and precipitate. After hydrolysis, the hydrolyzate is passed through a bed of XAD resin in a prepared column (previous step). The eluate is a purified collagen hydrolyzate which, when dried, is ready for isotopic analysis. The hydrolysis step is only performed on fossil bone

Supplies

- new, combusted culture tubes with new (not re-used) Teflon screw caps (2 tubes for each sample)
- combusted, disposable pipettes
- 6N HCL
- nitrogen or helium compressed gas
- clean 5 mm Teflon tubing fitted to regulator of compressed gas tank
- hot plate with hot block and thermometer
- extraction columns pre-loaded with XAD and filter disks
- 5.5 cm Whatman's glass filter disks and tape
- vortex evaporator (see supplemental section below)

Procedure

A. Hydrolysis

1- Add a few drops of HCL directly onto collagen in scintillation vials. Use as little HCL as possible since it has to be evaporated later. If only one portion of the collagen is to be hydrolyzed, while the remainder is curated, be certain to weigh the aliquot being hydrolyzed.

2- When all the collagen has dissolved, transfer it to culture tube using a pipette.

3- Rinse the pipette and the vial that contained collagen with a few drops of HCL to recover all residue; add to culture tube. There should only be about 2 to 3 ml of liquid in culture tube.

4- Evacuate air from the culture tube following the same procedure as Step 6 of the gelatinization process

5- Place culture tubes in hot block and heat for about 4 hours at 115 C

6- Precipitates will form quickly, so shake often. If possible, provide continuous shaking.

7. When heating is complete, immediately proceed to XAD extraction.

Notes and Hints

1- It is important to keep the amount of liquid used during hydrolysis to a minimum because it all has to be evaporated.

B. XAD Extraction

1- If syringe columns have been stored, allow one bed volume of HCL to gravity-flow through it column to hydrate the resin. Discard effluent.

2- Just before all of the HCL is drained, and when the samples are ready to be transferred, place the syringe over a clean, combusted, culture tube. This is the culture tube in which the filtered hydrolyzate will be collected.

3- Remove a sample from the hot block and pipette the liquid hydrolyzate a into syringe column (remember to label syringes and culture tubes with the specimen number).

4- Use a few drops of HCL and a fresh pipette to clean the culture tube and gather residual hydrolyzate. This is important if minute samples are being analyzed because collagen-derived peptides will be adhering to the glass.

5- Allow sample to flow by gravity. This will be slow— drop-by-drop— and it may be necessary to initiate the flow with a pipette bulb (however, the hydrolyzate should have been added to an already flowing volume of HCL). It is important to use gravity flow and not force the hydrolyzate through the resin bed because the resins only will retain short-chain peptides and other non-polar organic contaminants under low pressure. Applying pressure will force these contaminants out with the collagenous eluate.

6- Remove syringe column from the culture tube, label the column, and wrap it in parafilm if extracted contaminants are to be eluted later for analysis.

7-Wrap a glass filter disk around top of culture tube and secure with tape.

8- Dry samples in vortex evaporator set between 45 - 60 C.

9- Monitor samples carefully. Samples are dry when they are reduced to a thick brown mass that barely flows. Drying times can be quite variable, so check them often.

Notes and Hints

1- Because you will be performing multiple functions at once, it is easy to forget to label the culture tubes with the sample number. Also, the syringe column should be labeled with the sample number in the event that the retained contaminants are to be analyzed.

2- The hydrolyzed collagen will be brown to brownish-green. After it passes through the XAD resin and filter, however, it should be clear to light-yellow. When it is evaporated, it will be a brown viscous mass.

C. Drying Hydrolyzates Using a Vortex-Evaporator (and Vortex Evaporator Construction)

Supplies for Building Vortex-Evaporator:

-hot block w/ thermometer

-large benchtop flask-shaker

-vacuum desiccator

-flexible heating mantle that hot block fits into

-vacuum pump w/ hose; release valve for hose

-various size one-hole rubber stoppers

-glass vacuum trap and cold source (use cold chamber of lyophilizer or liquid nitrogen)

Construction of Vortex-Evaporator (Fig. 31):

A vortex-evaporator is used to dry materials that cannot be readily lyophilized, those that contain a solvent that is not very volatile, or those which cannot be heated. The vortex-evaporator essentially dries such samples by "boiling" them at very low temperatures and pressures. Low pressures are achieved by subjecting the samples to a vacuum which increases the samples' vapor pressure. Normally, liquids under a strong vacuum will bump (boil) as dissolved gasses are drawn out. The vortex-evaporator alleviates this problem by shaking (vortexing) the samples. Commercial vortex-evaporators can be purchased and occasionally they are found in biology laboratories. However, in this section I demonstrate how to construct one using commonly available items (Fig. 31).

The apparatus consists of a bell-shaped desiccator inside of which wrests a flexible mantle heater (the cloth-type used to warm large round-bottomed flasks). A hotblock to hold culture tubes is placed inside of the mantle, and the desiccator/heating unit is attached to a large flask-shaker. The heating mantle should be a size that fits well in the bottom of the desiccator, yet still holds the hot block snugly. The desiccator will need to be securely fastened to the top of the shaker using screws or bolts, so that it does not fall off during shaking.

The desiccator also needs to have two holes in it— one for the vacuum fitting and one for the mantle's power cord. Most desiccators have one or no holes, so holes may need to be drilled. Both holes need to be made air-tight. This is fairly straight forward for the vacuum connection— connect the vacuum hose to one of the holes in the desiccator using a plastic pipe connector and a one-hole stopper as a gasket.

The hole for the power cord can be made air-tight by running the cord through a one-holed rubber stopper (choose one that fits very tight). Then fit the stopper into the second hole in the desiccator. Both connections (vacuum and power) should be sealed with silicone between the rubber stopper and the desiccator.

A vacuum pump is attached to the desiccator via a hose that first runs through a two-part condenser in a cold trap. The trap of a lyophilizer can be used for this purpose. The cold trap is vital because it protects the pump from highly acidic vapors being drawn off of the samples. During use, a strong vacuum will develop in the desiccator chamber, so in order open it later, a pressure-release valve should be built into the vacuum line.

Operation

1- Preheat hot block (samples should be evaporated between 45 - 65 ° C, but block will need to be preheated to about 70° C since it cools down when samples are added and shaken).

2- Set up vacuum trap cold source (either refrigeration unit or liquid nitrogen).

3- Place culture tubes with hydrolyzed samples into hot block (samples should be covered by a glass filter disk secured by tape, according to step 7 in the hydrolysis procedure). Place cover on desiccator and start shaker, then start vacuum. Higher shaker speeds are better, since the hydrolyzate will become thicker with time and more prone to "bumping."

4- Monitor samples closely. Liquid will evaporate at a rate of about 2 - 3 ml per hour. Make sure the hot block does not cool down too much (although lower temperatures will only have the effect of prolonging the evaporation process). Some samples will become very dry-- nearly crusty-- while others can not be reduced beyond a semi-viscous syrup. Samples of the first type will tend to splatter on the sides of the culture tube, while the later do not splatter. It is acceptable to "over-dry" samples a bit, but this will tend to increase the splatter of "dry-type" samples. It can be difficult to collect samples for analysis from splattered hydrolyzates, so I recommend adding a few drops of HCl to such hydrolyzates and re-drying them.

5- When drying is complete, remove glass filter paper and cover the tubes with screw caps. Store samples in a refrigerator.

7. STORING AND ANALYZING COLLAGEN EXTRACTS

The extraction procedures produce dried collagen from modern bone and dried, hydrolyzed collagen from fossil bone. Both of these products can be stored for an indefinite period when kept in sealed containers and refrigerated. Modern collagen can be stored in the scintillation vial in which it was

lyophilized, and hydrolyzed collagen can be stored in the culture tube (capped) in which it was evaporated.

I do not describe procedures for preparing samples for spectrographic analysis because these techniques vary considerably depending on the mass spectrometer being used. However, I do have some suggestions for transferring and weighing-out sub-samples for analysis. First, dry collagen (modern bone) is very static-charged and not very dense, which will make it challenging to transfer and load the collagen. Sub-samples are best cut and transferred using a small stainless steel laboratory spatula or a fine tweezers (the spatula and tweezers should be cleaned with HCL (and dried) each time before they touch a sample). Since dried collagen is not very dense, a considerable volume often is required in order to load the proper mass. For instance, at UAF, I loaded 2 mg samples into small (~ 1 mm) aluminum cups for analysis on a Europa 20-20 continuous flow mass spectrometer; often, I had to compact the collagen sub-sample just to squeeze 2 mg into the cups.) Dried, hydrolyzed collagen (fossil bone) has the consistency of thick syrup and can be transferred using a spatula. Unlike un-hydrolyzed collagen, hydrolyzed collagen is dense and takes very little volume to meet the necessary weight requirements.

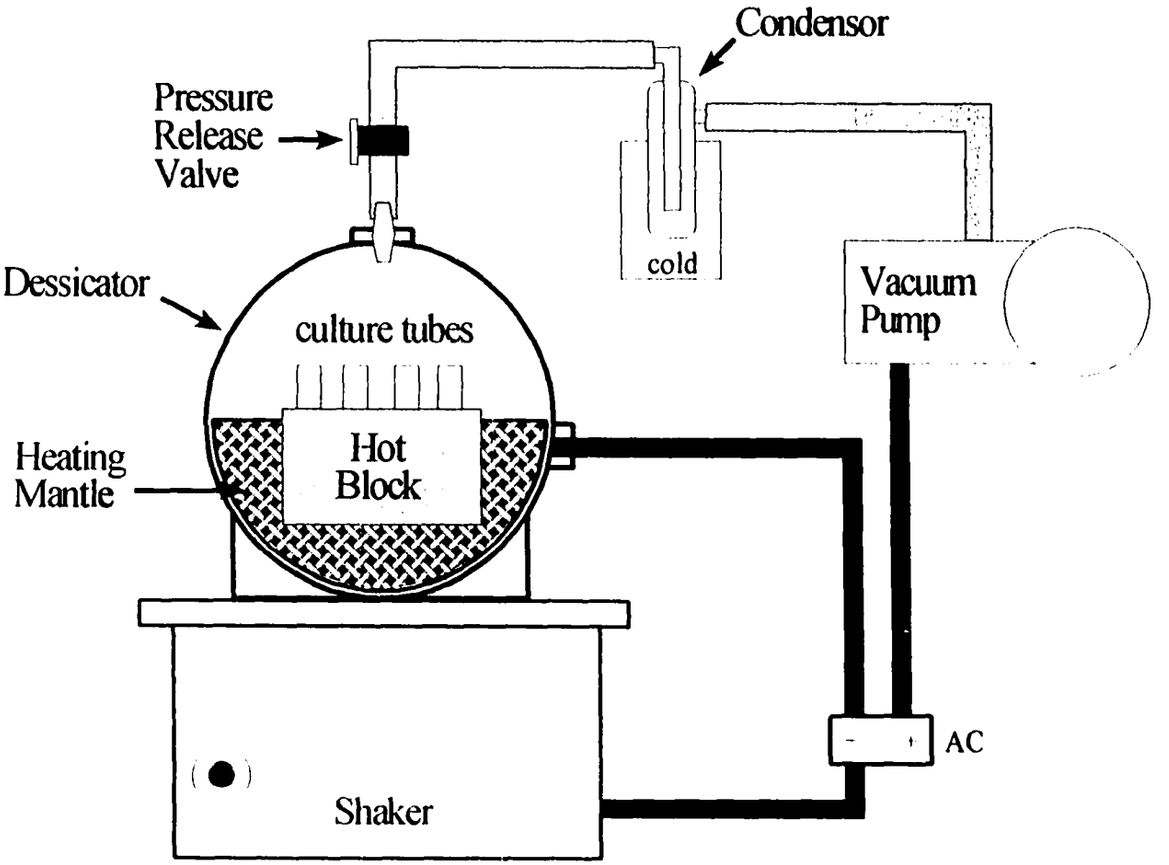

Figure 31. Vortex-Evaporator

SPECIMEN DATA SHEET (BONE COLLAGEN EXTRACTION)

LAB NO._____ **COLLECTION NO.**_____ **SPECIES:** _____

SKELETAL ELEMENT: ^{14}C AGE (lab #) _____

SITE INFO:

CONDITION: AGE: SEX: OTHER:

WEIGHING

SAMPLE WT_____ WT ANALYZED _____ WT CURATED _____

PRETREATMENT

scraped: _____ sonicated: _____ EtOH:_____ acetone:_____ chloroform _____

OTHER:

DECALCIFICATION

POWDERED, WHOLE, OR PIECES start time: end time: TOTAL TIME:

SUPERNATANT DESCRIPTION: RESIDUE DESCRIPTION:

QUALITATIVE ASSESSMENT:

BASE TREATMENT

TOTAL TIME:

SUPERNATANT DESCRIPTION: RESIDUE DESCRIPTION:

OVERALL CHANGE:

GELATINIZATION

TEMP: start time: end time: TOTAL TIME:

DESCRIPTION OF RESIDUE REMAINING UNDISSOLVED (COLOR):

DESCRIPTION OF SUPERNATANT (COLOR, AMOUNT REMAINING):

WT. LYOPHILIZED GELATIN: _____ % RECOVERY: _____

HYDROLYSIS

TEMP:_____

WT. USED: _____ start time:_____ end time:_____ TOTAL TIME:_____

PPT PRESENCE/DESCRIPTION:

SUPERNATANT DESCRIPTION:

XAD-2 EXTRACTION

COLOR OF RESIN: COLOR OF ELUATE:

METHOD OF DRYING:

COLOR/PURITY OF DRIED SYRUP:

MASS SPEC PREPARATION

TYPE OF SAMPLE: dried collagen hydrolyzate syrup

WT. OF CUP AND SAMPLE _____ RESULTS: C:N RATIO _____

WT. OF CUP _____ δ 13C _____

SAMPLE WEIGHT _____ δ 15N _____

NOTES AND OVERALL ASSESSMENT OF SAMPLE QUALITY

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